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1988

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HISTORICAL CHANGES IN ABUNDANCE OF SIX FISH SPECIES OFF SOUTHERN CALIFORNIA, BASED ON CALCOFI EGG AND LARVA SAMPLES

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ABSTRACT

We have developed annual indexes of larval abundances for five species sampled by the CalCOFI ichthyoplankton surveys from 1951 to 1985: northern anchovy, Pacific sardine, Pacific mackerel, jack mackerel, and Pacific whiting (or hake). We used a similar method to calculate annual indexes of egg abundances for a sixth species—Pacific saury. We pooled observations of larval densities within six geographic regions off southern California and northern Baja California, summarizing the data into region-month-year cells. We then used a multiplicative model of independent region, month, and year factors to predict the abundance in each cell. Under log-transform, the model becomes additive (i.e., log-linear) and was solved by analysis of variance (ANOVA). The ANOVA solution has the added advantage of accommodating missing values (43% of the possible 2160 cells lack observations). The antilogged month factors provided estimates of the mean temporal distribution of larvae over the months of the year. Antilogged region factors similarly provided the mean geographic distribution. Antilogged year factors from an ANOVA weighted by the monthly and regional distributions provided the annual indexes of abundance.

Abundance indexes for all six species show large fluctuations over the 35-year period. The index of northern anchovy larvae increased 50-fold from 1951 to the mid 1960s; since then it has fluctuated widely but without a trend. Indexes of Pacific sardine and Pacific mackerel decline from 1951 to the mid 1970s, and rise sharply thereafter, consistent with known increases in abundance. Indexes of jack mackerel and Pacific whiting are highly variable, and trends are difficult to identify. The index of Pacific saury eggs is high in the 1950s, is slightly lower for the next two decades, and drops severely in the 1980s. Changes in indexes of the latter three species are probably associated with environmental influences that have produced large-scale geographic shifts in spawning.

RESUMEN

Indices anuales de producción de larvas han sido desarrollados para 5 especies muestreádas por las expediciones de ictioplancton de CalCOFI: anchoveta del Norte (*Engraulis mordax*), sardina del Pacífico (*Sardinops sagax*), macarela del Pacífico (*Scomber japonicus*), jurel (*Trachurus symmetricus*), y merluza (*Merluccius productus*). Un método similar fue usado para calcular índices anuales de abundancia de huevos para una sexta especie, *Cololabis saira*. Las observaciones de densidad de larvas dentro de 6 regiones geográficas frente al sur de California y la region norte de Baja California fueron combinadas y resumidas en categorías de region-mes-año. En cada categoría se usó un modelo multiplicativo con factores independientes de región, mes y año para predecir su abundancia. Con una transformacion logarítmica, el modelo se volvió aditivo (i.e., lineal en escala logarítmica) y fue solucionado con un análisis de varianza (ANOVA). La solución ANOVA tiene la ventaja adicional de permitir la ausencia de datos (un 43% de las 2160 categorías posibles carece de observaciones). La función antilogarítmica de los factores mensuales entregó estimaciones de la distribución temporal promedio de larvas durante los meses del año. Similarmente, la función antilogarítmica de los factores regionales entregó la distribución geográfica promedio. La función antilogarítmica de los factores anuales de un ANOVA, ponderados por las distribuciones mensuales y regionales proporcionó índices anuales de abundancia.

Los índices de abundancia para las 6 especies muestran grandes fluctuaciones durante el periodo de 35 años. El índice de las larvas de la anchoveta del Norte aumentó 50 veces entre 1951 y mediados de la década de 1960; desde entonces ha fluctuado enormemente pero sin una tendencia clara. Los índices de la sardina y la macarela del Pacífico disminuyeron desde 1951 hasta mediados de la década de 1970, para después aumentar abruptamente, en forma consistente con aumentos en abundancia previamente establecidos. Los índices de *T. symmetricus* y *M. productus* son altamente variables y es difícil establecer un patrón. El índice de los hue-

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vos de *C. saira* es alto en la década de 1950, levemente inferior en las dos siguientes décadas, y cae considerablemente en la década de 1980. Los cambios en los índices de las últimas 3 especies están probablemente relacionados con factores ambientales que han producido desplazamientos geográficos de gran escala en el desove.

INTRODUCTION

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) have sampled fish eggs and larvae off the coast of California and northern Baja California since 1951. One of the goals of these and similar ichthyoplankton surveys has been to compile time series of abundances of the parent fish species (Moser et al. 1987; Smith and Moser 1988). In developing such abundance estimates there are many difficulties, ranging from uncertainty about the physiology of spawning activity to the statistics of highly patchy populations and incomplete sampling.

The present attempt to derive abundance time series from the CalCOFI data emphasizes development of a uniform methodology that can be applied to all species, independent of the amount of supplemental knowledge. We emphasize that these time series represent a first attempt for most of these species, and additional knowledge should lead to improved estimates for individual species. For example, Lo (1985) used information on growth rates and the size-frequency distribution of anchovy larvae to estimate their mortality rates and rates of parental egg production. The latter provided an improved index of adult abundance. However, we lack such supplementary information for most species. By comparing this "information-poor" analysis with complex, more reliable analyses of the same and/or supplementary data for well-studied species, we can infer the relative performance of this simple approach.

DATA AND METHODS

We summarized the CalCOFI egg or larval data by six geographical regions (Figure 1), for each month and year in which samples were taken. Although these regions were originally defined for purposes of stratifying distributions of anchovy larvae (Smith 1972; see Lo 1985 for current region definitions), they suffice for initial investigations of other species. It is important to note that the geographic regions used in this study do not necessarily cover the full spawning range of some of the species treated here. Because many sets of CalCOFI cruises began in November, we used a sampling year of November through October in this analysis.

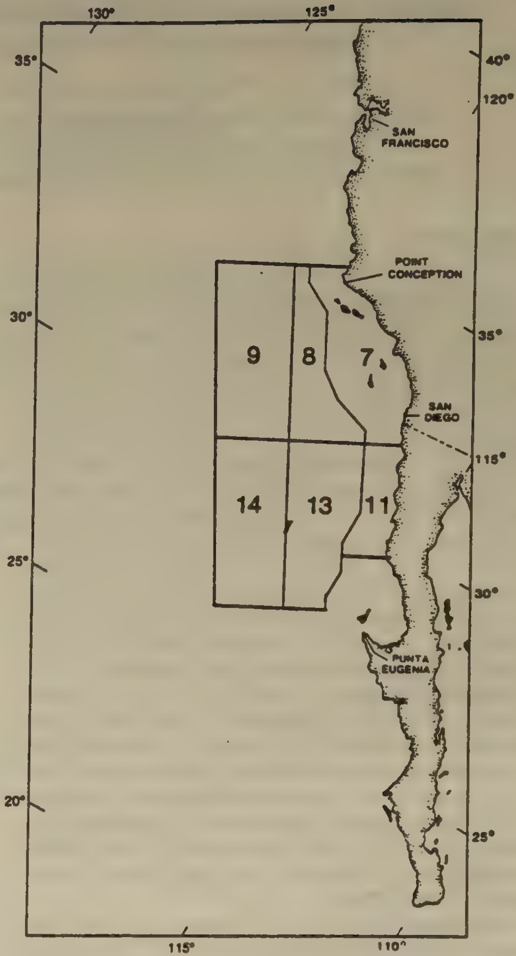

Figure 1. Location of the six geographic regions (7, 8, 9, 11, 13, and 14) used for pooling observations of larval densities.

Following the approach of Smith (1972), we calculated the average larval density for each of these year-month-region strata, or "cells," as the mean of the individual density estimates for all stations occupied within the cell[1] (see Kramer et al. 1972 for a general description of sampling methods; detailed data and changes in sampling are described in a series of publications beginning with Ambrose et al. 1987). During the study period 1951 to 1985, only six years (1970, 1971, 1973, 1974, 1976, and 1977) were not sampled at all. Many years were sampled thoroughly, especially 1951 through 1960. In the 30 "survey years" during the study period, a total of 1238 cells were sampled, which is about 57% of the possible 2160 cells. Missing values in the remaining 43% of the cells present statistical difficulties in developing reliable abundance estimates.

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[1] In cases where a cruise extended slightly into a second month, with very small numbers of stations occupied, we nominally combine the data under the adjacent principal month. These months were 11–62, 12–67, 5–68, 11–72, 11–74, 11–77, 4–82, 2–83, and 11–84. Data from 11–75, 12–75, and 11–85 were not used in the analysis.

A good solution to the problem of missing values is the method of maximum likelihood, but that method requires developing a complicated probabilistic model based on individual observations. The sheer number of observations (nearly 12,000) would present difficult computational problems. A simpler approach is to use an established model and statistical method that naturally accommodate missing values. For example, previous abundance indexes have used summation of data aggregated on a quarterly basis (Smith 1972), and linear interpolation has been proposed as a basis for estimating missing values (Smith 1978). Here we advocate use of a linear model, or analysis of variance (ANOVA), as an alternate approach that preserves monthly detail. For this application, ANOVA was used as an estimation tool rather than as a tool for testing statistical hypotheses. All computations employed a "main-effects" specification of the GLM procedure of SAS (see SAS Institute 1985 for technical details).

The ANOVA model predicts each cell value as the product of its respective month, region, and year factors. In effect, the month factors reflect the annual spawning cycle (shifted by the average age of the larvae, which usually is less than 0.5 months), and the region factors reflect the average geographic distribution of larval densities or spawning. The year factors reflect relative changes in overall production of eggs and their subsequent survival, and provide a tentative abundance index that may be useful for identifying long-term trends in abundance of the spawning stock within the geographic range of the sampling. In order to cast this multiplicative model as an ANOVA problem, the mean larval abundances were log-transformed (using natural logarithms). The resulting additive (log-linear) model is

$$\ln(N_{ijk} + 0.01) = \ln(R_i) + \ln(S_j) + \ln(T_k) + \text{constant} + \text{error} \qquad (1)$$

where R_i is the region factor ($i = 1, \ldots, 6$), S_j is the month factor ($j = 1, \ldots, 12$), and T_k is the year factor ($k = 1, \ldots, 30$). The solution is not unique, and the fitted constant depends on the scaling of the estimated factors; however, the relative relationships within a set of factors are independent of that constant (which is subsequently ignored), allowing their use as indexes. The quantity N_{ijk} is the mean abundance of larvae per 10 m^2 of sea surface. Because many observed values of N_{ijk} are zero, a constant was added before log transformation. Use of such a constant is a necessary evil in this log-linear approach and can distort the values of the estimated factors, especially for seasons or years with very low larval abundances. The added constant of 0.01 larvae/10 m^2 was near or slightly smaller than the smallest nonzero larval density measurable for a cell at typical sampling densities. Because the model is estimated under log transformation, the factors reflect geometric mean effects.

A further limitation of the simple ANOVA model is its disregard for interactions among factors. These interactions, such as geographic shifts in spawning areas as the season progresses, are known to occur (e.g., Kramer and Smith 1970). They can be addressed by a model such as

$$\ln(N_{kl} + 0.01) = \ln(C_l) + \ln(T_k) + \text{constant} + \text{error} \qquad (2)$$

where C_l is a combined month-region factor ($l = 1, \ldots, 72$). We used this model to examine month-region interactions for the peak months of spawning.

Moreover, the estimated time series of abundance indexes (T_k) were compared for the two models, providing a check on the amount of distortion introduced by the lack of interaction terms in equation 1. Shifts in spawning seasons or areas over the years also are known to occur, but formal recognition of these interactions in a model similar to equation 2 requires an excessive number of estimated parameters. Moreover, sample sizes for some individual factors become rather small, and a strong year-versus-region pattern of missing values makes estimation problematic; this is an area for further investigation.

In this log-linear ANOVA model with equal weighting of all cells, the year factors are highly influenced by months and regions that account for relatively few larvae. Accordingly, we used a weighted ANOVA to estimate the year factors. We chose a weighting scheme that allowed the influence of various months and regions to be made roughly proportional to their average contribution to the total year's spawning. Thus we approximated the weighting implicit in an additive "larval census" treatment, which is a sum of larvae over regions and seasons within a year (Smith 1972). Note that this weighted ANOVA should tend to be robust to error arising from variations in the duration of the spawning season (to the extent that duration is independent of spawner abundance), but may not be robust to error arising from overall shifts in spawning season or location among years.

In determining cell weights, we did not include the number of stations contributing to the cell mean; this modification is worth further consideration, but is somewhat more complicated than would first appear. For example, individual stations can vary substantially in amount of water filtered, as well as probable extrusion and/or avoidance by the larvae. The solution to these variable sample volume problems is likely to take the form proposed by Zweifel and Smith (1981), who weighted individual observations before averaging.

In addition to weighting the ANOVA to obtain the year factors, we restricted the months used in the ANOVA to peak spawning months. These months tend to have more and larger nonzero observations, reducing distortion due to addition of a constant for logarithmic transformation. On the other hand, using a small number of months increases difficulties arising from missing observations. Except for Pacific whiting, which has a brief spawning period, we included at least four months in the nominal peak spawning period in order to balance these two considerations.

The antilogged month and region factors from the previous unweighted ANOVA were used to calculate the weights for the weighted ANOVA, as well as to identify the peak spawning months. In accordance with equation 1, weights were calculated as the product of a month-weighting contribution and a region-weighting contribution. The month contribution consisted of the antilogged factors for the peak months, taken from the unweighted ANOVA and scaled to a unit sum. The region contribution was calculated similarly, except that antilogged region factors were first multiplied by the area of the corresponding region, in order to represent relative abundance of larvae in keeping with the analogy to a larval census (Smith 1972). The regions are shown in Figure 1, and their areas (taken from Lo 1985) are given in Table 1. Because of the month and region weights, observations in some cells are more important than others. A rough index of "effective sample size" is provided by the sum of cell weights for nonmissing values in each year (Table 2).

The added constant of 0.01 larvae/10 m^2 created a minimum possible abundance index, i.e., an index value obtained if no larvae were observed in any cell. We determined the approximate value of this minimum by supplying the ANOVA with an additional year of artificial data containing no positive observations. We assigned exceedingly small weights to these artificial data to avoid influencing the ANOVA results for the actual data.

The comparison of time series of year factors (T_k) as estimated by the simple and interaction models in equations 1 and 2 followed a procedure identical to that described above: We used an unweighted "main effects" SAS GLM procedure (ANOVA) to identify the peak months, and to provide cell weights accordingly. Weighted ANOVAs then produced time series of abundance indexes for the two models. We used the same cell weights for both models. Our use of peak months was especially important in this comparison, because the added constant in the logarithmic transformations in equations 1 and 2 would tend to create erroneous interactions in months and regions where larval densities were low. For a similar reason, the comparison was restricted to years that

TABLE 1
Region Factors from ANOVA with Equal Cell Weights, Reflecting Average Distribution of Larval Densities

	Region					
	7	8	9	11	13	14
Northern anchovy	0.828	0.024	0.007	0.121	0.020	—
Pacific sardine	0.478	0.053	0.078	0.173	0.144	0.074
Pacific mackerel	0.273	0.090	0.153	0.106	0.219	0.159
Jack mackerel	0.050	0.084	0.272	0.033	0.318	0.243
Pacific whiting	0.458	0.128	0.249	0.072	0.063	0.028
Pacific saury	0.214	0.129	0.336	0.036	0.157	0.128
Region area (10^3 n.mi.^{2})	20	12	29	9	21	29

TABLE 2
Effective Annual Sample Sizes for the Abundance Indexes

Species	Northern anchovy		Pacific sardine		Pacific mackerel		Jack mackerel		Pacific whiting		Pacific saury	
Year	N cells	Sum weights	N cells	Sum weights	N cells	Sum weights	N cells	Sum weights	N cells	Sum weights	N cells	Sum weights
1951	20	1.000	36	1.000	24	1.000	—	—	18	1.000	30	1.000
1952	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1953	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1954	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1955	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1956	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1957	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1958	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1959	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1960	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1961	12	0.601	24	0.659	18	0.707	18	0.595	12	0.540	18	0.652
1962	13	0.851	21	0.482	12	0.416	15	0.265	13	0.925	15	0.549
1963	15	0.691	24	0.654	18	0.733	18	0.620	15	0.540	18	0.741
1964	10	0.586	21	0.567	15	0.553	15	0.370	10	0.540	15	0.565
1965	9	0.653	23	0.656	18	0.683	20	0.567	9	0.515	17	0.580
1966	20	1.000	36	1.000	24	1.000	30	1.000	18	1.000	30	1.000
1967	—	—	9	0.277	9	0.394	9	0.203	—	—	3	0.096
1968	—	—	—	—	—	—	6	0.319	—	—	6	0.141
1969	15	0.939	29	0.860	21	0.847	23	0.721	15	0.810	23	0.835
1972	15	0.859	24	0.539	12	0.492	18	0.428	15	0.970	18	0.557
1975	10	0.414	24	0.710	18	0.840	24	0.833	10	0.460	18	0.531
1978	16	0.942	30	0.868	21	0.847	24	0.738	16	0.925	24	0.875
1979	17	0.943	—	—	—	—	—	—	17	0.928	18	0.708
1980	15	0.946	—	—	—	—	—	—	15	0.913	15	0.619
1981	17	0.983	31	0.892	21	0.847	25	0.743	17	0.872	25	0.858
1982	10	0.537	10	0.187	—	—	—	—	10	0.790	10	0.194
1983	5	0.309	5	0.095	—	—	—	—	5	0.447	5	0.103
1984	17	0.958	32	0.891	—	—	—	—	17	0.975	26	0.909
1985	11	0.595	11	0.299	—	—	—	—	11	0.743	11	0.358

are relatively well sampled, i.e., that lacked no more than about one month's observations during the peak spawning period.

RESULTS

In all six species cases, the time series of abundance indexes estimated from equation 1 and the month-region interaction model of equation 2 are nearly indistinguishable, indicating that no serious distortion results from the model in equation 1. Because of the lack of differences, we do not include detailed results of these comparisons in this report.

Northern Anchovy (**Engraulis mordax**)

The unweighted ANOVA showed a protracted spawning season (Figure 2), with the peak months of February through May accounting for 85% of the larvae seen during the year. The two inshore

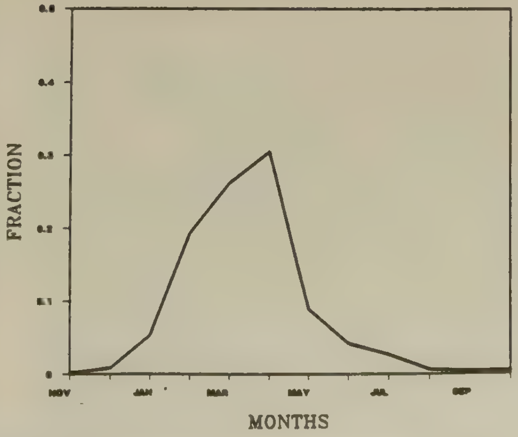

Figure 2. Seasonal distribution of northern anchovy larvae.

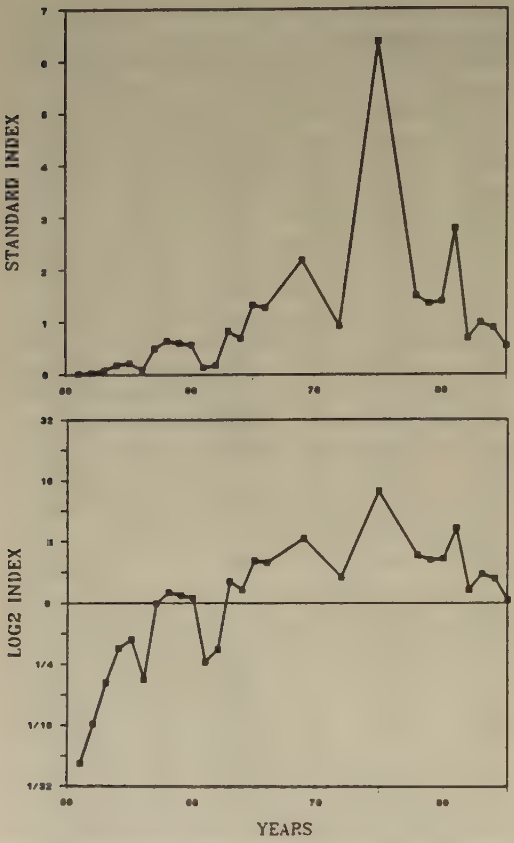

Figure 3. Time series of abundance indexes for northern anchovy larvae. *Upper*: arithmetic scale, mean = 1; *lower*: $\log_2$ scale.

regions account for 95% of the total larvae (Table 1). Because the southern, offshore region 14 accounts for very few larvae (less than 0.1%), we omitted it from the weighted ANOVA.

Overall, the abundance indexes (Figure 3) were quite similar to the historical egg production time series developed by Lo (1985) from much more complete information including the size distribution of larvae. The main exception was the index value for 1978, which we estimated to be much lower than Lo's value. However, Lo's estimate for 1978 (unlike other years in the series) is based on an assumed preliminary value regarding egg retention by the bongo net (Lo 1983). This value was later revised based on experiments conducted in 1984 (N. Lo, SWFC, pers. comm.); the updated egg retention value was used by Methot (1986) and gives a 1978 value that is similar to the index value developed here.

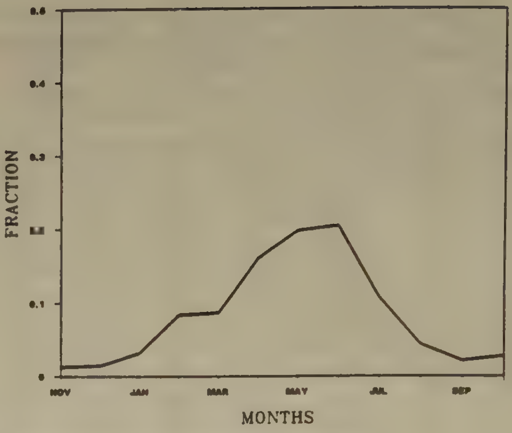

Figure 4. Seasonal distribution of Pacific sardine larvae.

Pacific Sardine (Sardinops sagax)

The long apparent spawning season (Figure 4) is partially an artifact of the added constant; sardine larvae have been scarce for many of the 35 years covered by the surveys. The main spawning period is April, May, and June, but a broad peak appears to extend from February through July and includes at least 85% of the larvae seen during the year. About half of the larvae occurred in inshore southern California waters (region 7), and 80% occurred in combined nearshore regions 7, 11, and 13 (Table 1). As in the case of nonpeak spawning months, the importance of the offshore regions (8, 9, and 14) was probably exaggerated because of the added constant.

The minimum abundance index corresponding to "no larvae" was only slightly below the estimates obtained for the 1970s ($\log_2$[minimum] = −3.99; Figure 5). Our abundance estimates for this low period are therefore not reliable, and the population may well have reached lower levels of abundance than those suggested by our analysis. However, for the first half of the time series, the indicated decline is in agreement with the trend in estimates of abundance derived from fishery catch data (MacCall 1979).

Pacific Mackerel (Scomber japonicus)

As in the case of the sardine, the long apparent spawning season is partially an artifact of the added constant and the low abundance of larvae experi-

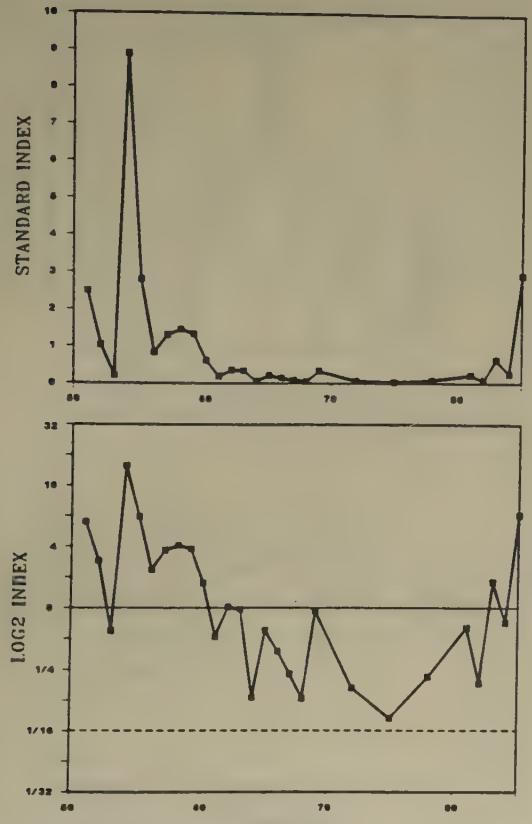

Figure 5. Time series of abundance indexes for Pacific sardine larvae. *Upper*: arithmetic scale, mean = 1; *lower*: $\log_2$ scale. Dashed line indicates minimum abundance index due to added constant.

enced over much of the time series. Peak spawning is in May through July (Figure 6); however, we included April as a fourth month to increase the sample size. The period April–July accounts for at least 68% of the larvae seen during the year (the true average spawning season is probably more peaked than that calculated here, because of the added constant). Larvae were distributed rather evenly among the six regions (Table 1), but again this evenness also may be exaggerated by the added constant. The index value for 1975 is very near the minimum possible estimate ($\log_2$[minimum] = −4.26; Figure 7); as in the case of the sardine, lower levels of abundance may have been reached than are indicated by our analysis. The sudden increase in 1978 and 1981 is consistent with the recent resurgence of the population (MacCall et al. 1985).

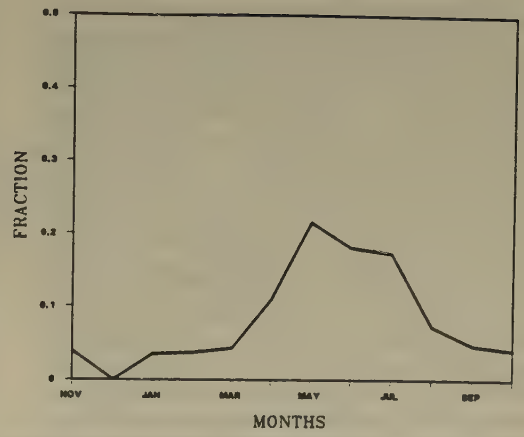

Figure 6. Seasonal distribution of Pacific mackerel larvae.

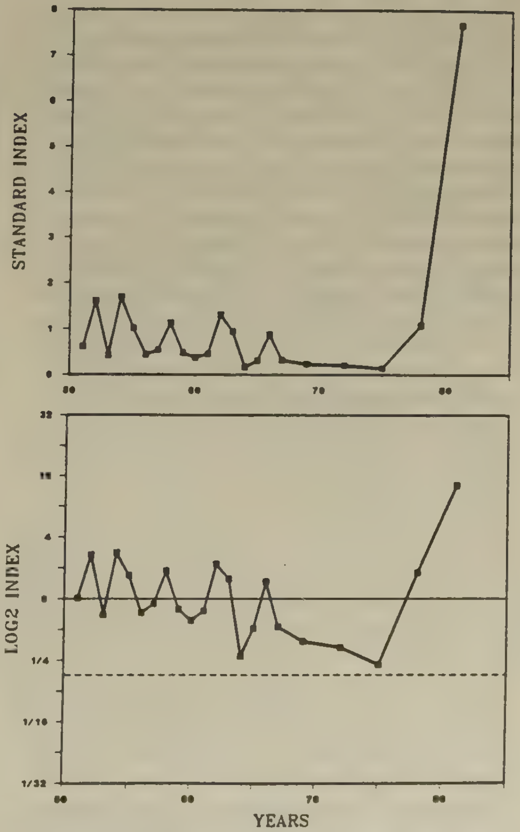

Figure 7. Time series of abundance indexes for Pacific mackerel larvae. *Upper*: arithmetic scale, mean = 1; *lower*: $\log_2$ scale. Dashed line indicates minimum abundance index due to added constant.

Jack Mackerel (**Trachurus symmetricus**)

There is a sharp peak of larval abundance in May and June (Figure 8), but for purposes of the ANOVA, we used a peak spawning season of March through July, accounting for 97% of the annual total. Larvae are mostly offshore, with regions 9, 13, and 14 accounting for 83% of the total (Table 1). At the time this study was conducted, the CalCOFI data for 1951 were incomplete, so 1951 was not included in the calculations. The time series of larval abundance indexes (Figure 9) is highly variable, and does not correspond closely to the time series of mean larval abundances compiled by MacCall and Stauffer (1983), which included information from waters off central California. We also note for jack mackerel as well as for some other species that the variability in this index must be far greater than the true variability of a population composed of long-lived individuals.

Pacific Whiting or Hake (**Merluccius productus**)

The very short spawning season of whiting (Figure 10) prevents extending the analysis beyond February, March, and April, during which 97% of the larvae are observed. Also, 84% of the larvae were observed in the northern three regions (Table 1). Ahlstrom (1969) notes that through 1966, the standard CalCOFI plankton samples, which reached a maximum depth of about 140 m, "evidently do not encompass the complete vertical distribution of hake eggs and larvae at some stations." The depth of the standard CalCOFI plankton samples was extended to about 210 m beginning in 1969, at which time the netting was also changed from silk to an equivalent but more uniform nylon

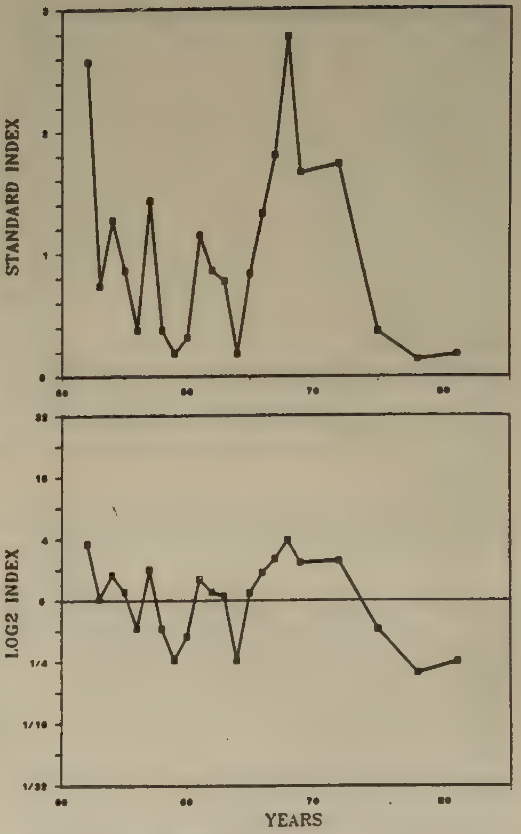

Figure 9. Time series of abundance indexes for jack mackerel larvae. *Upper*: arithmetic scale, mean = 1; *lower*: $\log_2$ scale.

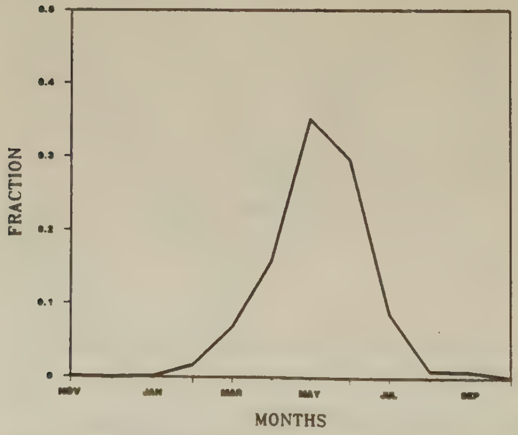

Figure 8. Seasonal distribution of jack mackerel larvae.

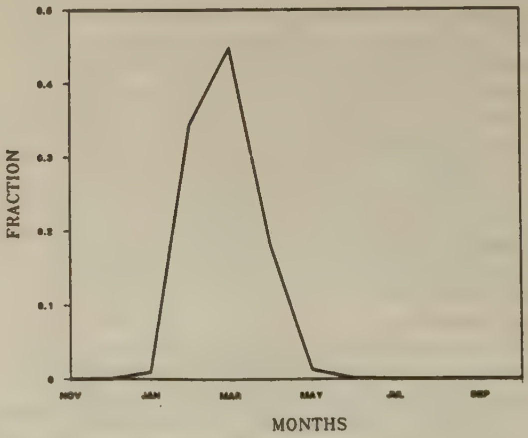

Figure 10. Seasonal distribution of Pacific whiting larvae.

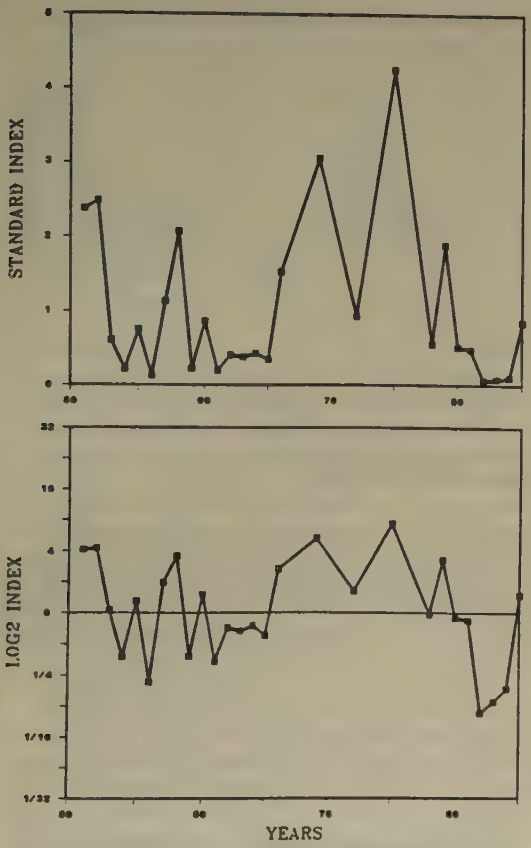

Figure 11. Time series of abundance indexes for Pacific whiting larvae. *Upper*: arithmetic scale, mean = 1; *lower*: $\log_2$ scale.

mesh (Smith 1974). The index of whiting abundance (Figure 11) is higher during the period following these sampling changes, but changes in actual abundance cannot be discounted; the index increases in 1966, immediately prior to the sampling changes, and the low levels of 1982–84 are lower than any seen previously. The index for whiting is highly variable, and does not agree with abundance estimates based on fishery data (Hallowed et al. 1987), which show a major increase during the 1980s.

Pacific Saury (**Cololabis saira**)

Egg abundance is very high in April (Figure 12), but we assumed a more extended peak spawning season of February through June, covering 90% of the annual total eggs observed. The geographic distribution of eggs is fairly even, except for a scarcity in region 11 (Table 1). There has been an irregular decline in abundance of saury eggs in the study area since the early 1950s, with eggs being nearly absent since 1980 (note that the latter indexes approach the minimum value possible in this analysis, $\log_2$ [minimum] = -5.24; Figure 13). We cannot determine from internal evidence if the change is due to a northward contraction of the spawning distribution, or if it is a population decline. Few years during the transition period were sampled; the southern regions are incompletely covered; and the geographic coverage of this study is very limited with respect to the overall distribution of saury spawning.

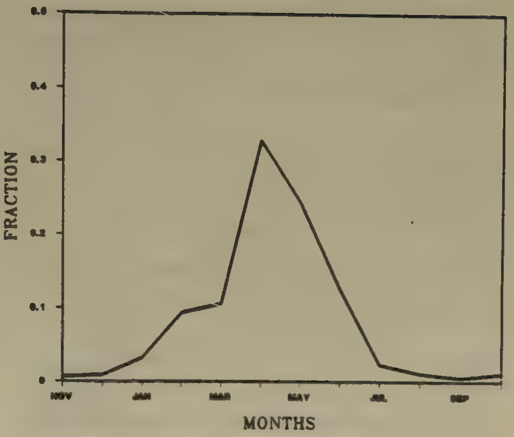

Figure 12. Seasonal distribution of Pacific saury eggs.

DISCUSSION

The ANOVA method is successful in that it accommodates missing values and produces easily derived indexes of abundance. The method does have shortcomings, especially in treating geographic or seasonal shifts in distribution among years, which seems to be a major source of error. Inclusion of data from waters off central California might have clarified some northward shifts, but that area has a high incidence of missing values, and its contribution would be correspondingly imprecise. In the case of rare larvae, results are biased by the added constant in equation 1. Of course, there is little information content in years where few or no larvae are encountered.

Several improvements on this log-linear or ANOVA approach should be investigated. Missing values may be better accommodated by the EM algorithm (Haberman 1974). Even better would be the maximum likelihood approach, which would include variable sample sizes among cells, but re-

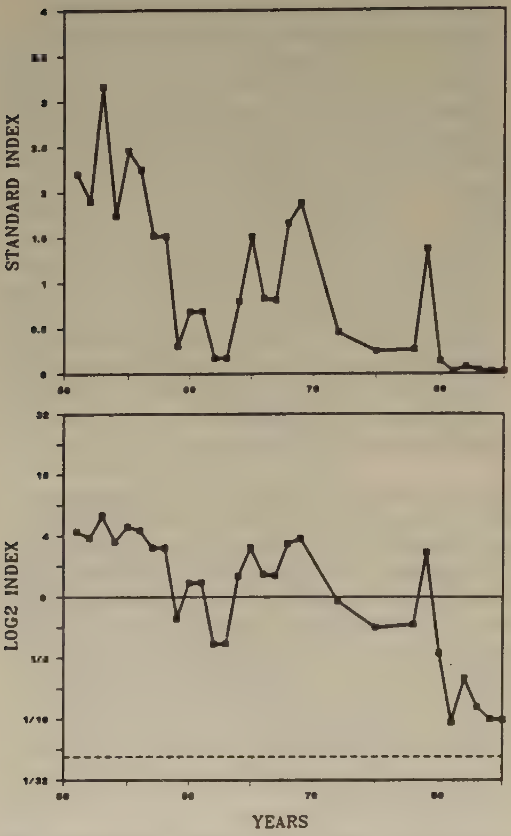

Figure 13. Time series of abundance indexes for Pacific saury eggs. *Upper:* arithmetic scale, mean = 1; *lower:* $\log_2$ scale. Dashed line indicates minimum abundance index due to added constant.

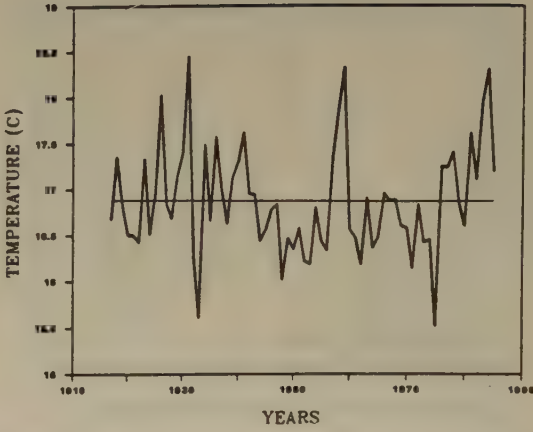

Figure 14. Time series of annual average Scripps Pier water temperatures. Horizontal line is long-term mean.

sults would still be imprecise. Methods for accounting for region-year and region-month interactions should be investigated. The performance and robustness of various approaches could be investigated by means of simulated data. Regions could be redefined in a manner appropriate for each species, and regions off central California should be included.

Major changes in the indexes of three species—Pacific sardine (increase), Pacific mackerel (increase), and Pacific saury (decrease)—have occurred in the last decade, and there is a suggestion that the indexes for Pacific whiting and jack mackerel also have decreased. The California Current has tended to be warmer since the mid 1970s. Annual average Scripps Pier temperatures (Figure 14) have risen by about one-half a degree Celsius, ending a cool period extending from the early 1940s. The warming has been more consistent in the offshore regions of the California Current (Cole and McLain, in press). Pacific saury and jack mackerel spawn relatively northward and offshore, and we speculate that the declines in abundance indexes for these two species are probably the result of northward spawning shifts in response to this warming. For this reason, we prefer to interpret the recent declines in these indexes as shifts in distribution rather than decreases in population abundance.

The spawning area of Pacific whiting similarly shifted northward in recent years (Paul Smith, SWFC, pers. comm.), presumably also in association with the oceanic warming. We also interpret the recent decline in the abundance index for whiting as the result of a northward shift in spawning, with a substantial portion of the population now spawning off central California. Contrary to the decrease in this larva-based index, fishery-based estimates of whiting abundance show a substantial increase during the 1980s, but declining sizes at age in the U.S. fishery independently suggest a northward shift of the resource (Hallowed et al. 1987).

On the other hand, the increases in indexes for sardine and Pacific mackerel, which also coincide with the warming, are definitely associated with respective increases in population abundance (Wolf and Smith 1986; MacCall et al. 1985). Again, these increases have been accompanied by northward shifts in the spawning distributions as indicated by the larval distributions.

The time-series of these six species underscores the importance of long-term monitoring. Had the CalCOFI surveys ceased in 1975, these time series would be far less interesting. Of the six species, only the index for anchovy shows little change after 1978, and that index shows a very large change in the first decade of the time series. Thus, a time series spanning only 25 years would risk missing major population or environmental changes, whereas a series spanning 35 years seems, at least in this case, to have detected major changes.

Isaacs (1976) emphasized the importance of "regimes" in contrast to the usual assumptions of stability (or stable distributions of environmental conditions) underlying fishery models. The temperature history in Figure 14 suggests three major temperature regimes: warm from the beginning of observations in 1916 to the early 1940s (>30 yr), cold to the mid 1970s (ca. 35 yr), and then warm again. The earlier warm regime preceded the era of physical and biological monitoring. The physical and biological changes associated with the recent warming indicate that Isaacs's concern with regimes was justified. Long-term monitoring, such as has been conducted by CalCOFI, is vital to understanding these phenomena.

ACKNOWLEDGMENTS

In addition to the many people who have contributed to the CalCOFI program over the past 35 years, we wish to thank several people who contributed particularly to the present paper. Celeste Santos Methot compiled the source data from the CalCOFI data files. Rich Charter, John Michno, and Kevin Colwell provided computer programming and data base management support. Geoff Moser and his co-workers provided summaries of larvae from recent CalCOFI cruises virtually as the identifications were being completed. Finally, we thank the Ocean Assessments Division, National Ocean Service, NOAA, for supporting this investigation.

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SOME PROBLEMS IN ESTIMATING POPULATION SIZES FROM CATCH-AT-AGE DATA

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ABSTRACT

A new method for estimating population sizes from catch-at-age data is given. The method treats the observed population sizes as missing data and uses a combination of the Kalman filter and the EM algorithm to derive maximum likelihood estimates of the parameters and minimum mean square error estimates of the population sizes. The algorithm does not assume that the observation errors and the errors in the population dynamics are uncorrelated with equal variances, which is a common assumption of existing techniques. A new parameterization for both recruitment and fishing mortality is given, based on smoothness priors. Recruitment (or fishing mortality) is estimated as a nonparametric function of time by calculating an "optimal" tradeoff between goodness-of-fit and smoothness of the function. The algorithm allows for multiple sources of observations (fishing, surveys, etc.) and allows for missing data in the observations, which can arise if the different sources of the observations occur on different time scales. An example suggests that the new algorithm may better capture variation that is important when using the population estimates to study the role of the environment (or other exogenous variables) on the population dynamics.

I can address the motivation of this paper by considering a slightly modified version of a model proposed by Collie and Sissenwine (1983). Assume that the underlying population dynamics satisfy

$$N(a+1, t+1) = [N(a,t) - C(a,t)]\,\tilde{m} + w(a,t)$$

$$a = 1, A \qquad (1)$$

where $N(a,t)$ is the number of fish age a at time t, $C(a,t)$ is the catch of age a fish at time t, $\tilde{m} = exp(-m)$ is the mortality rate and the vector $w(t) = (w(1,t), \ldots, w(A,t))^{\tau}$ is a sequence of independent, identically distributed normal random vectors with mean 0 and covariance matrix Q, and for any vector a, the notation a^{τ} denotes the transpose of the vector. We assume that the initial population vector $N(0)$ is gaussian with a mean of μ and covariance Σ.

The population itself is not observed. Instead we observe that

$$n(a,t) = q(t)N(a,t) + v(a,t) \qquad (2)$$

where q is an unknown parameter and the vector $v(t) = (v(1,t), \ldots, v(A,t))^{\tau}$ is a sequence of independent, identically distributed normal random vectors with mean 0 and covariance matrix R. It is assumed that $E(v(t)\ w(t)^{\tau}) = 0$; that is, the observation error and the underlying randomness in the population are uncorrelated. There is some interest in the value of the estimates of the $q(t)$ (or if mortality is to be estimated, in the estimate of $\tilde{m}$) but the major interest lies in estimating the unobserved population sizes $N(a,t)$. The estimates of the $N(a,t)$ should reflect not only the trend in the population, much as a regression might, but also the period-to-period variation of the population, such as might be related to environmental changes. This will be the emphasis throughout the paper.

The model described in Equations (1) and (2) differs from that of Collie and Sissenwine (1983) in that I do not assume that the mortality rate is known; here I allow the underlying population dynamics to be random, and the observation errors in Equation (2) to be additive rather than multiplicative. For known $\tilde{m}$, Collie and Sissenwine (1983) suggested minimizing

$$\sum_{t=1}^{T} \sum_{a=1}^{A} (v(a,t)^2 + w(a,t)^2) \qquad (3)$$

over the parameters (in our notation) $\theta = (q, N(t))$

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where $N(t)$ is the vector of unobserved population sizes. The concern here is not whether the multiplicative or additive form of the model is more correct, but rather what elements of the model are data, what are parameters, and how to calculate appropriate estimates of each.

If there were all-seeing observers, both the population process $N(t)$ and the observation process $n(t)$ would be available as data. Equations (1) and (2) imply a sequence of conditional probability distributions $f_N(N(t + 1) \mid N(t), \theta_1)$ and $f_n(n(t) \mid N(t), \theta_2)$, where θ_1, θ_2 are parameters of the distributions to be estimated. Assuming additive gaussian errors, then θ_1 would include the mean vector $FN(t)$ and a covariance matrix that can be calculated recursively (see below). The mortality rate $\tilde{m}$ serves as a constraint on the form of the estimates of the mean vector, much as in the theory of regression. Similarly, the parameters for the observation process are a mean vector $H(t)N(t)$ and a covariance matrix, where $H(t)$ in this case depends on the parameters $q(t)$ that constrain the estimates of the mean vector. With an all-seeing observer, both $n(t)$ and $N(t)$ are realized values of random vectors and hence, are the data to be used to estimate the unknown parameters of the distributions, θ_1 and θ_2.

Thus, the unobserved population sizes are most appropriately treated as missing data. The estimation scheme proposed by Collie and Sissenwine (1983) treats the $N(t)$ as parameters to be estimated. Little and Rubin (1983, 1987: sec. 5.4) showed that treating missing data as parameters in likelihood equations does not produce maximum likelihood estimates of the parameters unless the proportion of missing data approaches zero as the sample size increases. This is because much of the asymptotic theory of maximum likelihood estimation depends on the number of observations becoming large, relative to the number of parameters. Little and Rubin (1983, 1987) showed that for a regression-like situation, the bias due to treating data as parameters can be quite large.

The alternate approach discussed by Little and Rubin (1983, 1987) is to integrate out the missing data from the complete data likelihood and maximize this function over the parameters as usually defined in estimation theory. This is the approach taken by Shumway and Stoffer (1982a), who used the EM (expectation-maximization) algorithm of Dempster et al. (1977) and Kalman filtering to derive maximum likelihood estimates for the parameters of the model and minimum mean square error estimates of the missing data.

I can explain some of the problems with estimating Equations (1) and (2), using the likelihood of Equation (3). Under the gaussian assumptions of the model, the complete data log-likelihood is given by (Shumway and Stoffer 1982a)

$$-\frac{1}{2}\log|\Sigma| - \frac{1}{2}(N(0) - \mu(0))^{\tau}\,\Sigma^{-1}$$
$$(N(0) - \mu(0)$$
$$-\frac{T}{2}\log|Q| - \frac{1}{2}\sum_{t=1}^{T}(N(t) - FN(t-1))^{\tau}$$
$$Q^{-1}(N(t) - FN(t-1))$$
$$-\frac{T}{2}\log|R| - \frac{1}{2}\sum_{t=1}^{T}(n(t) - H(t)N(t))^{\tau}R^{-1}(n(t)$$
$$- H(t)N(t)) \qquad (4)$$

where $F = \tilde{m}I$ and $H(t) = q(t)I$. Similarly, the complete data log-likelihood in Equation (3) by substitution is

$$-\sum_{t=1}^{T} \| N(t) - FN(t-1) \|^2 + \| n(t)$$
$$- H(t)N(t) \|^2. \qquad (5)$$

Collie and Sissenwine (1983) noted that their estimation scheme assumes that the process and observation errors have the same variance. However, from Equations (4) and (5) it can be seen that they make the stronger and unlikely assumption that both the errors in the population dynamics and the errors in the observation process are uncorrelated. Further, we can see from Equation (4) that when the $N(t)$ are treated as parameters, the estimates of the $N(t)$ depend on the observed data $n(t)$ for $t = 1,T$. Following Shumway and Stoffer (1982a), the expected log-likelihood conditioned on the observed data comprises three parts: a term due to estimating the expected value of the initial population size,

$$-\frac{1}{2}\log|\Sigma| - \frac{1}{2}tr\,\{\Sigma^{-1}[P(0|T) + (N(0) - \mu)$$

$$\times (N(0) - \mu)^{\tau}]\}, \qquad (6)$$

a term due to the unobserved dynamics,

$$-\frac{1}{2}\sum_{t=1}^{T}\log|Q(t)|$$

$$-\frac{1}{2}\sum_{t=1}^{T} tr\,\{Q(t)^{-1}[(N(t|T) - FN(t - 1|T))$$

$$\times (N(t|T) - FN(t|T)^{T}$$

$$+ P(t|T) + FP(t - 1|T)F^{\tau} - P(t - 1|T)$$

$$\times F^{\tau} - FP(t, t - 1|T)]\}, \qquad (7)$$

and a term due to the observation process,

$$-\frac{1}{2}\sum_{t=1}^{T}\log|R(t)|$$

$$-\frac{1}{2}\sum_{t=1}^{T} tr\{R(t)^{-1}[(n(t) - H(t)N(t|T))$$

$$\times (n(t) - H(t)N(t|T))^{\tau}$$

$$+ H(t)P(t|T)H(t)]\} \qquad (8)$$

where $N(t|s)$ denotes

$$N(t|s) = E[N(t) \mid n(1), \ldots, n(s)], \qquad (9)$$

$P(t|s)$ denotes

$$P(t|s) = E[(N(t) - N(t|s))$$

$$\times (N(t) - N(t|s))^{\tau} \mid n(1),$$

$$\ldots, n(s)], \qquad (10)$$

and $P(t,t - 1|s)$ denotes

$$P(t,t - 1|s) = E[(N(t) - N(t|s))$$

$$\times (N(t - 1) - N(t - 1|s))^{\tau}$$

$$\times \mid n(1), \ldots, n(s)]. \qquad (11)$$

As shown in Equations (6) through (8), the proper estimates of the $N(t)$ and the related covariance matrices should be conditional expectations based on all of the data rather than on only the data up to time t. Assuming that all quantities are calculated properly, estimates that include only the data up to time $t - 1$ are termed "predicted" estimates, estimates that include only the data up to time t are termed "filtered" estimates, while estimates given all the data are termed "smoothed" estimates. I shall show below that the appropriate formulas for predicted, filtered and smoothed estimates differ significantly. Thus using Equation (5) as the likelihood and treating the $N(t)$ as parameters does not produce proper estimates of the $N(t)$.

In the rest of this paper, I review state-space models and methods for estimating both the parameters and the unobserved components of the model. A very readable background for what follows is chapter 3 in Shumway (1988). The estimation scheme described does not require that the components of R, Q, and Σ have equal variance and are uncorrelated. Explicit estimates of these matrices are given. Then I show that a variety of age-based models proposed in the literature can be formulated as a state-space model, but that the formulations as presented make the same error of treating the unobserved components as parameters, and assume zero covariance in the errors. Auxiliary information as in Deriso et al. (1985) can be put into this format. And I show that the state-space formulation can include multiple observations of the population, but where some of the observations are missing. This can arise when the population is observed from fishing and from a variety of surveys, but some of the surveys are not done every year. This is essentially the problem discussed in Methot[2]. I give true maximum likelihood estimates for this model, allowing the different observation processes to have different error structures and estimate the relative weight that should be given each. This is a significant advance over the procedure in Methot (fn. 2).

A related paper is the analysis of Brillinger et al. (1980) who use a modified Kalman filter and maximum likelihood estimation to estimate the average birth and death rates and population structure of Nicholson's blow-fly data when only total numbers of births and deaths at any time are available. In their model, knowing the births is equivalent to knowing the recruitment at each time period and the deaths are observed directly without error. Also, they appear to use the filtered estimates of the population structure, while the smoothed estimates are the minimum mean squared estimates given all the data. P. Sullivan[3] in his Ph.D. dissertation independently developed a length-based fishery model using Kalman filtering and maximum likelihood estimation.

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[2] Methot, R. 1986. Synthetic estimates of historical abundance and mortality for northern anchovy, *Engraulis mordax*. Adm. Rep. LJ-86-29. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

I reiterate that the models considered here assume additive errors, while much of the existing literature prefers multiplicative errors, particularly for the observation equation. The basis of this preference appears to be that models with multiplicative errors have given a better "fit" to the data for other estimation schemes. In these estimation schemes the errors are assumed to have equal variances and are assumed to be uncorrelated. The better fit found for multiplicative errors in these algorithms may be due to these assumptions on the error variances. In effect, the errors are being scaled by the observed data which suggests that the assumption of equal variances is incorrect. In the present formulation I assume additive errors, but I can allow for errors with unequal variances, for errors that depend on the size of either the observed catch $n(a,t)$ or on the unobserved population $N(a,t)$, and for missing observations, and I can obtain simple to compute standard errors of the estimated underlying population sizes. The algorithm is also simple to program. If multiplicative errors are assumed, it is more difficult to calculate exact maximum likelihood estimates. Approximate likelihood methods (such as the extended Kalman filter) have known undesirable properties. When the full richness of the assumptions allowed in additive error models is used, it is an open question if multiplicative errors are to be preferred.

STATE SPACE MODELS

The State-Space Model can be written in the form (Jazwinski 1970; Anderson and Moore 1979; Ljung and Soderstrom 1983):

$$x(t) = F(t)x(t-1) + B(t)u(t-1) + Gw(t) \tag{12}$$

$$y(t) = H(t)x(t) + v(t) \tag{13}$$

where $x(t) = (x_1(t), \ldots, x_p(t))^{\tau}$ is the p-dimensional unobserved state of the system; $u(t) = (u_1(t), \ldots, u_p(t))^{\tau}$ is a p-dimensional vector of deterministic inputs; $y(t) = (y_1(t), \ldots, y_q(t))^{\tau}$ is the observed data of the system; $w(t) = (w_1(t), \ldots, w_p(t))^{\tau}$ is a sequence of zero mean normal vectors with common covariance matrix Q; $v(t) = (v_1(t), \ldots, v_q(t))^{\tau}$ is a sequence of zero mean normal vectors with common covariance matrix R; and F, B, G, and H are appropriately dimensioned matrices that may depend on an unknown parameter vector θ. Note that q, the dimension of the observation vector, can be larger than p, the dimension of the state vector. Thus several different observation processes of the underlying dynamics are allowed.

Using the same notation as in Equations (9) and (10), the predicted, filtered, and smoothed estimates of the state vector and the covariance matrices can be calculated recursively as follows: for prediction and filtering,

$$x(t|t-1) = F(t)x(t-1|t-1) + Bu(t-1) \tag{14}$$

$$\begin{aligned} P(t|t-1) = {} & F(t)P(t-1|t-1)F(t)^{\tau} \\ & + GQ(t)G^{\tau} \end{aligned} \tag{15}$$

$$\begin{aligned} K(t) = {} & P(t|t-1)H(t)^{\tau} \\ & \times (H(t)P(t|t-1)H(t)^{\tau} + R(t))^{-1} \end{aligned} \tag{16}$$

$$\begin{aligned} x(t|t) = {} & x(t|t-1) + K(t) \\ & \times (y(t) - H(t)x(t|t-1)) \end{aligned} \tag{17}$$

$$P(t|t) = P(t|t-1) - K(t)H(t)P(t|t-1) \tag{18}$$

where $x(0|0) = \mu$ and $P(0|0) = \Sigma$, and for smoothing,

$$J(t-1) = P(t-1|t-1)H(t)^{\tau}(P(t|t-1))^{-1} \tag{19}$$

$$\begin{aligned} x(t-1|T) = {} & x(t-1|t-1) + J(t-1) \\ & \times (x(t|T) - x(t|t-1)) \end{aligned} \tag{20}$$

$$\begin{aligned} P(t-1|T) = {} & P(t-1|t-1) + J(t-1) \\ & \times (P(t|T) - P(t|t-1))J(t-1)^{\tau}. \end{aligned} \tag{21}$$

The predicted state variable $x(t|t-1)$ differs from the quantity often used as the predicted value in the fisheries literature in that it is based on the last period's filtered estimate rather than on the last period's predicted estimate. (For example, Deriso et al. (1985) suggested using backward VPA or cohort analysis to obtain predicted values.) The filtered estimate $x(t|t)$ is a weighted average of the predicted value of $x(t|t-1)$ and the observed error in estimating $y(t)$, where the weighting term $K(t)$ (the Kalman gain matrix) is regression-like. Similarly, the covariance of the estimate, as measured by $P(t|t-1)$, increases due to the prediction, but decreases by the amount $K(t)H(t)P(t|t-1)$ after the observation has been made. The smoothed estimate $x(t|T)$, which is the correct estimate of the underlying population (it satisfies the conditional expectation), is found by a backward recursion on the filtered estimates, where the filtered estimate is adjusted by a regression on the error between the smoothed and predicted estimates of the following period. Thus the smoothed estimates correct the predicted estimates both by the error in predicting the observed data as well as by the error in predicting the underlying population when using the filtered estimates of the underlying population. The square roots of the diagonal terms of the various P matrices produced by the Kalman recursions are the standard errors of the predicted, filtered, and smoothed estimates of the population.

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[3] P. Sullivan, Center of Quantitative Sciences, University of Washington, Seattle, WA 98195, pers. commun. 1988.

Equations (12) and (13) are the basic form of the state-space model. It is a simple extension to the model to allow any of the matrices F, B, G, or H to be nonlinear functions of the past values of the $y(t)$ (see, for example, Shiryayev (1984), section VI.7), to allow the error vectors $w(t)$ and $v(t)$ to depend on past values of the $y(t)$ (Shiryayev 1984), or to allow the $v(t)$ to depend on the underlying state vector $x(t)$ (Zehnwirth 1988).

In a typical fisheries problem, the matrix $H(t)$ represents fishing. If some age-specific measure of effort $E(a,t)$ is known, then $H(t)$ is a diagonal matrix with $E(a,t)$ on the diagonals. Or it may be assumed that the exploitation rate is of the form $s(a)E(t)$, where $E(t)$ is known and the $s(a)$ values are to be estimated. Then for given values of $s(a)$, the matrix $H(t)$ has $s(a)E(t)$ on its diagonals. The matrix $F(t)$ is formed in a similar manner to represent the population dynamics.

In some parameterizations, it is assumed that a known vector is subtracted from the state vector either before or after the effect of F on the population. For example, the known vector might be the catch from the previous time period. The extension to the Kalman filter in this case is straightforward, an example of which can be found in Jazwinski (1970). Essentially, all predicted estimates of the state are corrected by the constant amount. The covariance and gain calculations are unaffected by the known vector.

The Kalman filter, Equations (14) through (21), assumes that the matrices F, B, G, H, R, Q, and Σ, and the vector μ are known. For fisheries problems, the matrices F and H usually depend on a set of parameters to be estimated (e.g., $F = mI$), and R, Q, and μ are to be estimated. Let θ be a vector containing the parameters that F and H depend on, and let $\Theta = (\theta, R, Q, \mu)$ be the total parameters of the model. Shumway and Stoffer (1982a) showed that conditional on Θ, the complete data likelihood is given by Equation (4). They apply a result of Dempster et al. (1977), which shows that maximum likelihood estimates of the parameters can be obtained by finding the conditional expectation (the E-step) of the complete data likelihood with respect to the missing "data" (in this case the missing data are the sufficient statistics of the normal distribution) and alternately estimating the expected value of the missing data, and then maximing the likelihood (the M-step) using the completed data. Shumway and Stoffer (1982a) showed that the expected conditional log-likelihood is given by Equations (6) through (8). All of the terms in this likelihood, for a given value of Θ, can be found by the Kalman filter. Moreover, given these values, the maximization problem is a deterministic one.

If we assume that the matrix F is independent of time and unrestricted, then Shumway and Stoffer (1982a) showed that the maximization step is accomplished by setting

$$F = S_t(1)S_{t-1}(0)^{-1} \tag{22}$$

$$Q = (S_t(0) - S_t(1)S_{t-1}^{-1}(0)S_t(1)^{\tau})/T \tag{23}$$

$$\begin{aligned} R = T^{-1} \sum_{t=1}^{T} [&(y(t) - H(t)x(t|T) \\ &\times (y(t) - H(t)x(t|T))^{\tau} \\ &+ H(t)P(t|T)H(t)^{\tau}] \end{aligned} \tag{24}$$

$$\mu = x(0|T). \tag{25}$$

where $$S_t(j) = \sum_{t=1}^{T} (P(t, t-j|T) + x(t|T)x(t-\mathrm{j}|T)^{\tau}). \tag{26}$$

Shumway and Stoffer (1982a) gave a recursive formula for calculating $P(t, t-1|T)$ while performing the backward smoothing recursion.

If we assume that F is constrained to be of the form $F = \tilde{m}D$ where $\tilde{m}$ is a constant and D is a known matrix, then Shumway and Stoffer (1982b) showed that

$$Q = (C - \tilde{m}BD^{\tau} - \tilde{m}DB^{\tau} + \tilde{m}^2DAD^{\tau}) \qquad (27)$$

$$\tilde{m} = \frac{tr(Q^{-1}BD^{\tau})}{tr(Q^{-1}DAD^{\tau})}. \qquad (28)$$

Equations (27) and (28) can be solved by taking an initial guess for $\tilde{m}$, then iteratively solving for Q and $\tilde{m}$ until the values converge.

Finally, we can make explicit the effect of assuming equal variances and no covariances for both $w(t)$ and $v(t)$. For given estimates of Q and R, since both are square, symmetric matrices, they can be factored as

$$Q = U\,DU^{\tau}$$

$$R = LL^{\tau}$$

where U is an upper triangular matrix, D is a diagonal matrix, and L is the lower triangular square root of R. To obtain an underlying population dynamic that has an uncorrelated error vector $\tilde{w}(t)$ and uncorrelated observations with variances of 1, we make the following transformations:

$$\tilde{G} = GU$$

$$\tilde{y}(t) = L^{-1}y(t)$$

$$\tilde{H}(t) = L^{-1}H(t)$$

$$\tilde{v}(t) = L^{-1}v(t)$$

and replace G, w, y, H, and v in Equations (14) through (21) with the transformed values. Then $\tilde{v}(t)$ has covariance matrix I, and $\tilde{w}(t)$ has covariance matrix D. The assumption that both the error in the dynamics and in the observations are equal, further constrains the values of D to be identical. This is a very strong assumption.

AN EXAMPLE

As an example of these methods, I use the data for Pacific mackerel published in Parrish and MacCall (1978). I emphasize that I am only using these data for illustrative purposes and do not claim to be making a careful, thorough reexamination of the problem. Though $\tilde{m}$ can be estimated using Equation (28), I assume that the value of $\tilde{m}$ is known a priori. If I were to use a different value of $\tilde{m}$, it would be difficult to judge to what extent the new estimates differ solely due to the different mortality rate, rather than due to the estimation scheme. I assume, as in the reference, that the mortality rate m is equal to 0.5, so that the F matrix in my notation is a matrix with a value of 0.6065 in position $(i, i-1)$, $i = 2, \ldots, 7$, corresponding to the underlying dynamics for age groups 1 through 6.

Recruitment in Pacific mackerel is highly variable. I want to obtain estimates of recruitment that accurately reflect this variability while still being consistent with the observed data. Also, I do not want to a priori assume a functional relationship between recruitment and population size. To this end, I assume that the recruitment time series, after taking differences of a given order, is a random variable, i.e.,

$$\nabla^k r(t) = w(t) \qquad (29)$$

where $w(t)$ is a normal random variable with a mean of zero and with an unknown variance σ^2 and ∇^k denotes kth order finite differencing. Akaike (1979) originally showed that this formulation is the discrete equivalent of fitting a spline to the data (in this case as a function of time), where the estimate of the variance σ^2 expresses the tradeoff between the degree of smoothness in the fitted curve with fidelity to the observed data. In this approach, k and the variance of $w(t)$ are treated as hyperparameters of the model. A fitting criterion such as AIC is then used to determine the best value of k given the data. Following Kitagawa and Gersch (1984), I could use smoothness priors to more generally decompose recruitment as

$$r(t) = T(t) + S(t) + \xi(t) + w(t) \qquad (30)$$

where $T(t)$ is a trend term (as in Equation (29)), $S(t)$ is a seasonal term, and $\xi(t)$ is an irregular stationary term. A decomposition such as Equation (30) would be useful, for example, in modeling the monthly anchoveta recruitment considered in Mendelssohn and Mendo (1987). However, for convenience in this paper, I restrict recruitment to be of the form in Equation (29).

The relationship between this "smoothness priors" approach, "smoothing splines", and other penalized likelihood methods is discussed further for a variety of contexts in Brotherton and Gersch (1981), Kitagawa and Gersch (1984, 1985, 1988), Ansley and Kohn (1986), and Kohn and Ansley (1987, 1988). Wahba (1977) and O'Sullivan (1986) discussed the relationship between generalized cross-validation, penalized likelihood functions, and determining the tradeoff between smoothness and fit.

For $k = 0$, Equation (29) models recruitment as a random variable around a fixed but unknown mean value. For $k = 1$, Equation (29) models recruitment as a random walk with unknown mean level and drift (variance). Higher values of k have similar interpretations. Values of k higher than two or three rarely need to be considered, since these include the discrete equivalent of cubic splines. Cubic splines can approximate most functionals (in this case of time) to a reasonable degree of accuracy.

For this example, I assume $k = 1$, so that

$$r(t) = r(t - 1) + w(t) \tag{31}$$

which is a random walk with unknown variance. (A more complete analysis of this data would probably also include an irregular stationary term as in Equation (30) and determine the "best" order of differencing using a given criterion.) Equation (31) can be incorporated into the state space model by letting the (1, 1) element of the matrix F be equal to 1. The matrices $H(t)$ are diagonal matrices whose values are calculated from table 13 in Parrish and MacCall (1978). Because I am assuming that the estimates of F are known, then the value of Q for the M step is maximized as

$$T^{-1}[S_t(0) - S_t(1)F^{\tau} - FS_t(1) + FS_{t-1}(0)F^{\tau}]. \tag{32}$$

As in Parrish and MacCall (1978), I treated age groups 4 through 6 as fully selected by the fishery, and will refer to these age groups as "adults". Similarly, I refer to the number of age-1 fish at the start of the season as the number of recruits. I assume that F and $H(t)$ are known, so the estimation problem is reduced to determining the means of the initial population sizes and the values of the two covariance matrices Q and R.

The resulting maximum likelihood estimates of Q and R (Tables 1, 2) show that the variances of the error terms differ by up to two orders of magnitude, hardly meeting the usual assumption of equal variances. Moreover, the covariances (expressed as correlations in the tables) are quite high, so that using $\frac{1}{\sigma}$ as a weighting factor will not be adequate. The predicted, filtered, and smoothed estimates of the adults (Fig. 1) are very similar, reflecting that the errors have been "filtered out" over time by the population dynamics.

TABLE 1.—Estimated values of the matrix Q presented as a variance-correlation matrix. The diagonal terms are the variances, and the off-diagonal terms are the cross-correlations.

	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
Age 0	8.72E+09	−0.9075	0.2429	0.0592	0.1785	−0.2096	0.0249
Age 1		4.59E+09	−0.1750	−0.0574	−0.1658	0.1803	−0.0432
Age 2			1.07E+09	0.0396	0.2416	0.1109	0.0675
Age 3				5.28E+08	0.7030	0.5964	0.3140
Age 4					1.90E+08	0.6717	0.3944
Age 5						3.08E+07	0.4854
Age 6							2.18E+06

TABLE 2.—Estimated values of the matrix R presented as a variance-correlation matrix.

	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
Age 0	7.30E+07	−0.0497	0.8505	0.7367	0.6594	0.5120	−0.4019
Age 1		2.62E+07	0.1594	0.0896	−0.0544	−0.3411	0.4325
Age 2			4.95E+06	0.6764	0.6412	0.3830	−0.2418
Age 3				3.43E+06	0.7286	0.4908	−0.2260
Age 4					7.11E+05	0.5708	−0.2030
Age 5						2.05E+05	−0.1331
Age 6							5.40E+04

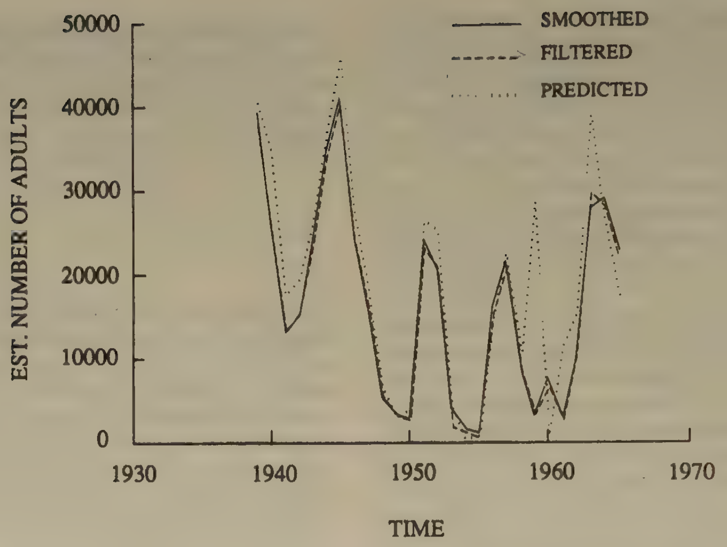

FIGURE 1.—Estimated number of adults, 1939-65, using values from Parrish and MacCall.

The predicted, filtered, and smoothed estimates of the recruits (Fig. 2), unlike those of the adults, are not similar. The filtered and smooth estimates are often indistinguishable, but there are some years (such as 1941 and 1943) where there are significant differences. The predicted values are very smooth, tending to emphasize the trend in the recruitment. In an analysis of recruitment estimates produced by standard cohort analysis of the anchoveta off Peru, Mendelssohn and Mendo (1987) found the estimates

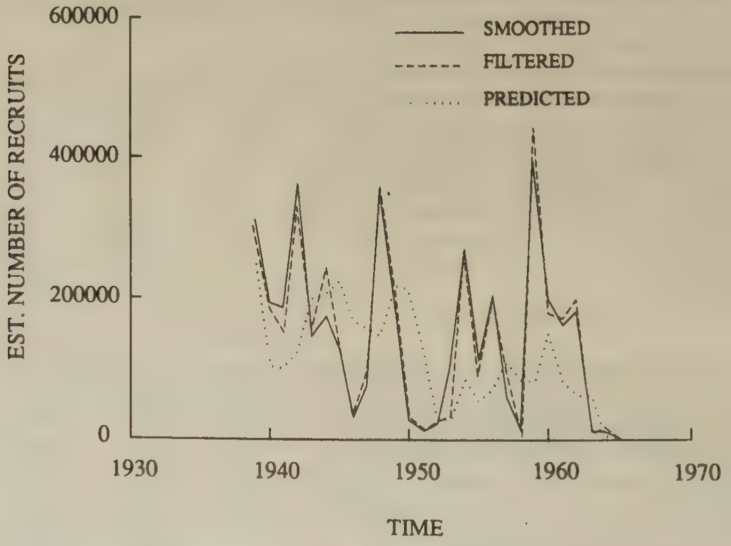

FIGURE 2.—Estimated number of recruits, 1939-65, using values from Parrish and MacCall.

to be far too smooth. The results of this present example may explain their observation. If these values were used in a subsequent analysis, say to determine the role of the environment on recruitment, a totally false picture of this relationship could emerge. I emphasize that the predicted estimates are calculated from the previous season's filtered values, whereas it is often true in the fisheries literature that the predicted values are estimated from the previous predicted values, rather than from the filtered values. Direct comparison with the estimate in Parrish and MacCall (1978) are difficult because restricting recruitment to be of the form (Equation (29)) with k fixed, rather than the more general form (Equation (30)) with k variable, may not be appropriate for the Pacific mackerel data. But overall, their estimates tend to resemble the smoother trend of my predicted estimates.

RELATIONSHIP TO OTHER LITERATURE AND A NEW PARAMETERIZATION

If the models are restricted to additive errors, then most of the simpler difference equation models proposed in Collie and Sissenwine (1983), Deriso et al. (1985), Fournier and Archibald (1982), Fournier and Doonan (1987), and among others can be formulated as I did. Some of these models assume recruitment is a nonlinear function of the underlying population, which cannot be handled in this model without some modifications (suggested below). However, all of these authors treat the underlying population sizes as parameters of the data rather than as missing data. As discussed earlier, it is questionable whether this will produce proper estimates of the underlying populations. Biases from treating missing data as parameters in a regression setting are explicitly discussed in Little and Rubin (1983, 1987).

A very broad class of possible models that can be selected to model catch-at-age data are given by Schnute (1985). He correctly identified the values that are parameters of the difference equations he discusses, and these are sufficient for estimating the likelihood (if evaluated properly). However, if we assume observation error, then it can be shown (see, for example, Shumway 1988) that the innovations are determined by predictors calculated from the previous period's filtered, rather than predicted values. Moreover, the minimum mean squared error estimates of the underlying populations, as discussed earlier, are the smoothed estimates. It appears that Schnute (1985) used the predicted or, at best, the filtered estimates of the underlying populations.

A popular parameterization that appears to have been first suggested by Doubleday (1976) is to assume that the observation matrix $H(t)$ is of the form $H(t) = \{s(a)f(t)\}$ where $s(a)$ is an age-dependent selectivity factor and $f(t)$ is a time-dependent exploitation rate. These values can be found by using a minimization routine during the M-step of the algorithm. However, it should be noted that the estimate of $f(t)$ for each t will depend on R and that the estimate of R will depend on both $s(\cdot)$ and $f(\cdot)$, so that either R, s, and f should be solved for together, or else they should be successively solved for using Equation (7) while holding the other parameter values fixed.

Alternatively, Equation (7) can be differentiated. Then for given values of $f(t)$, the optimum value of the vector $s(a)$ at each iteration are the diagonals of the matrix S given by

$$S = AB^{-1} \tag{33}$$

where $A = \sum_{t=1}^{T} y(\mathrm{t})x(t|T)^{\tau}f(t)$, and $B = \sum_{t=1}^{T} f^{2}(t)$ $(P(t|T) + x(t|T)x(t|T)^{\tau}$. However, this is an unconstrained estimate and does not guarantee that $s(a)$ is between (0,1). It can be shown that the optimal solution is to set $s(a)$ at zero if $s(a)$ is negative or to 1 if $s(a)$ is greater than 1.

For fixed values of $s(a)$ and R, Equation (7) is maximized when $f(t)$ takes the value

$$f(t) = \frac{tr(R^{-1}y(t)x(t|T)^{\tau}S^{\tau})}{tr(R^{-1}S(P(t|T) + x(t|T)x(t|T)^{\tau})S^{\tau})} \tag{34}$$

where the matrix S is as above. This is the unconstrained solution. The constrained solution again is to force the estimate to lie within the closed interval (0, 1) as with the estimate of the $s(a)$. Since the estimates of R, $s(a)$, and $f(t)$ are interrelated, I have found it to be a workable procedure to first estimate Q as given above and then for a given number of iterations, iteratively solve for $f(t)$ then $s(a)$. When these values stabilize, estimate R using the formula given above. While this procedure does not necessarily maximize Equation (7), it is sufficient for the generalized EM algorithm the new values increase the function given in Equation (7).

As with the original estimates, the smoothed and filtered estimates of recruitment (Fig. 3) are close

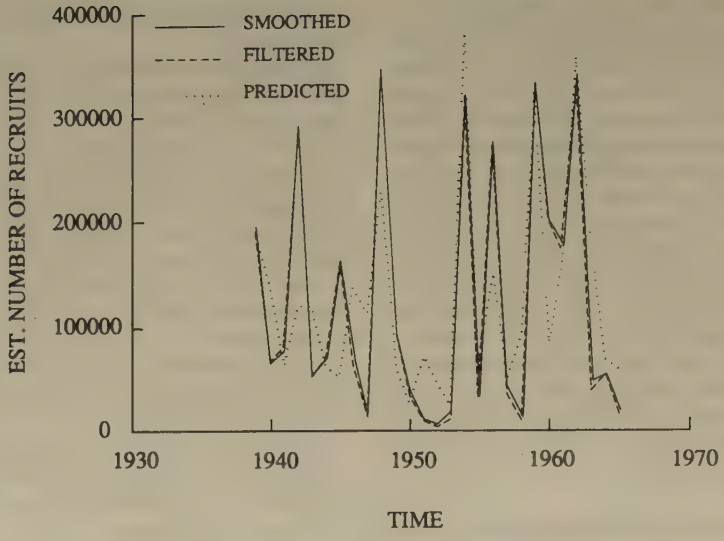

FIGURE 3.—Estimated number of recruits 1939–65, assuming $q(a, t) = f(t)s(a)$.

to each other, while the predicted values are too smooth. The estimated values of $f(t)$ (Fig. 4) generally decline with time. All three estimates are significantly different from the previous estimates. Years where relative highs and lows occur differ, showing the sensitivity of this class of models to the assumed form of the H matrix. Since the estimates of R, $s(a)$ and $f(t)$ are interrelated, I suspect that the parameter estimates are highly correlated and hence unstable. While I have not calculated the parameter covariance matrix, it should be checked for any serious analysis using these techniques.

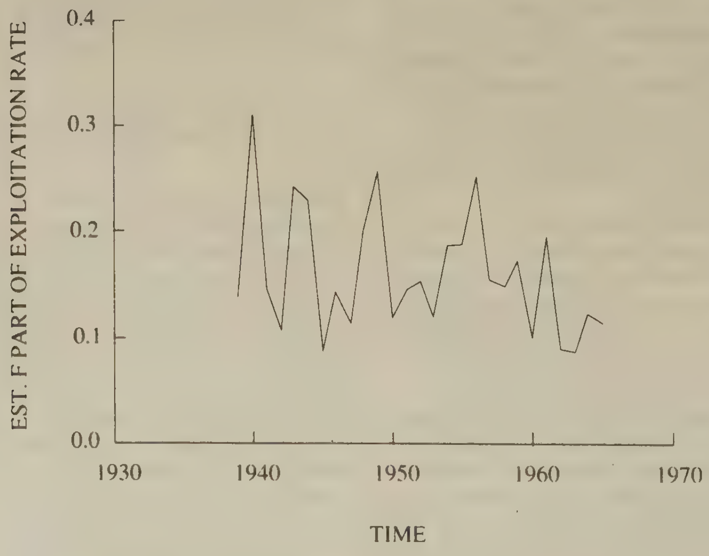

FIGURE 4.—Estimated values of $f(t)$ when $q(a, t) = f(t)s(a)$.

While the parameterization $H(t) = \{f(t)s(a)\}$ greatly reduces the number of parameters, I still face the same problem as when I treated the unobserved population as parameters: each new period adds another parameter to the model. The model still appears to be overparameterized, and the asymptotic theory for maximum likelihood estimation may be invalid.

As with the recruitment estimates, the number of effective parameters can be reduced by adding a smoothness prior on $f(t)$. However, $f(t)$ is a proportion and not likely to be a normal variable. The $f(t)$ are also constrained to lie in the interval $(0, 1)$, so a transformation to an unconstrained variable would also be desirable. If $f(t)$ is a binomial random variable then arcsin $(\sqrt{f(t)})$ is approximately normal with nearly equal variance. This suggests the transformation of variables

$$f(t) = \sin^2(e(t)) \tag{35}$$

where $e(t)$ is an unconstrained normal variable. Then the smoothness prior becomes

$$\nabla^k e(t) = w(t) \tag{36}$$

(a smoothness prior that includes a seasonal component or irregular stationary part, as in Equation (30), can also be used), and for any age class, the observation equation becomes

$$y(a,t) = s(a)\sin^2(e(t))x(a,t). \tag{37}$$

The underlying population dynamics must also be expanded to include the smoothness prior constraint (Equation (36)).

Unfortunately, the observation equation is no longer linear in the state vector. The smoothness prior is a prior distribution on the $f(t)$, and a full Bayesian analysis can be done to obtain the overall distribution. The variance of $w(t)$ is then treated as a hyperparameter in the analysis.

A simpler approach is to evaluate the filter equations approximately by using any one of a number of nonlinear filters (see Anderson and Moore 1979). One that is easy to implement, given the nonlinearities in this problem, is the extended Kalman filter (EKF), which at each time period just linearizes all the nonlinear terms around the value of the predicted state vector. The EKF, however, can have divergence problems and is not guaranteed to find the true penalized likelihood estimates.

When using the EKF, it works to make a forward and backward pass of the filter given the current estimates of $f(t)$ and $x(t|T)$, and then to estimate $s(a)$ and R as before. I tested the algorithm on the mackerel data with $k = 1$ in the constraint (Equation (36)). The resulting estimates (Fig. 5) are similar to the previous estimates, but the estimated values of $f(t)$ (Fig. 6) are less variable with a stronger trend than before. It is clear from Figure 5 that the

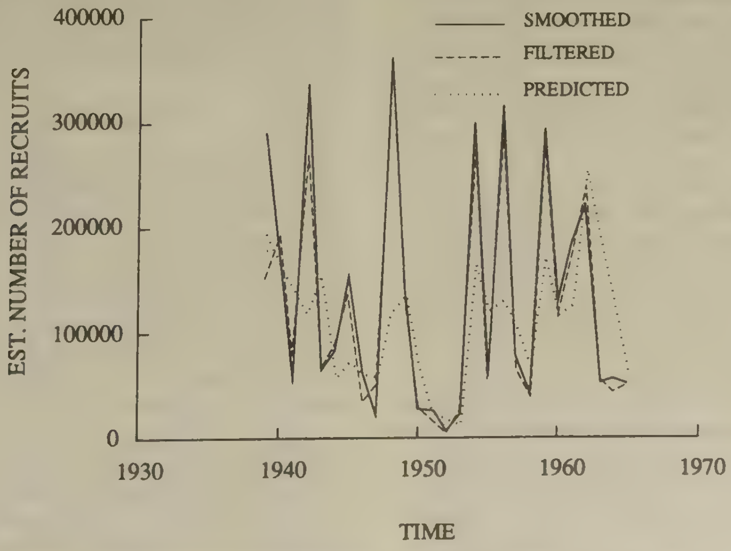

FIGURE 5.—Estimated number of recruits using a first order spline for estimating $f(t)$.

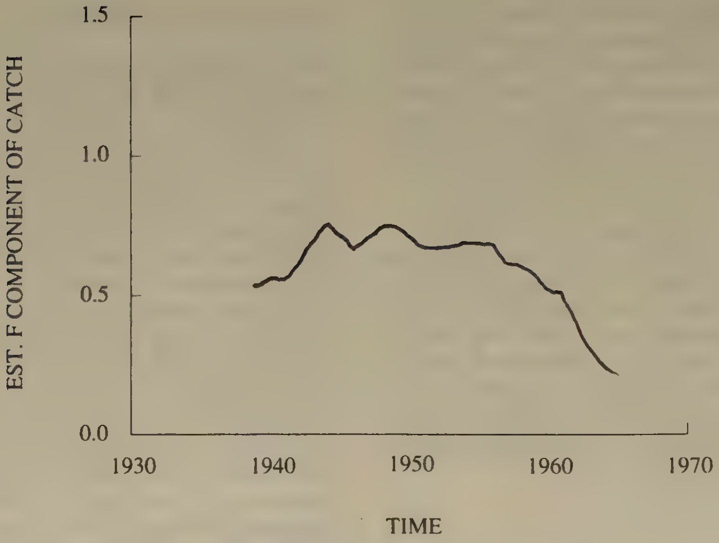

FIGURE 6.—Spline estimates of $f(t)$.

smoothness prior estimate has shifted some of the variation in the observed data to variations in the underlying population dynamics rather than variations in $f(t)$. Further research needs to be done to see which of these estimates is the most "valid".

The EM algorithm in general can be sensitive to the initial values given the parameters (see Wu 1983), and I have found that the fixed value of Σ can also affect the estimates. Initial combinations of μ, $f(t)$, and $s(a)$ that are totally inconsistent with the observed catch data can cause the algorithm to find a local maximum. This can be avoided by experimenting with several, very different starting values and determining if they converge to the same estimates.

If recruitment is thought to be a linear function of the previous population size, then there is no problem including this in the Kalman filter. If recruitment is a nonlinear function of the previous population, then the EKF can again be used to approximately determine the conditional expectations needed for the EM algorithm.

If information is available from a variety of sources, say from fishing and from surveys, as in Methot (fn. 2), then each of the vectors and matrices can be partitioned to represent this situation. For example, let $y_s(t)$ be the observed catches from a survey and $y_f(t)$ the observed catches from fishing. Let $y(t)^\tau = (y_s(t), y_f(t))^\tau$, and partition the H matrix similarly. Then the diagonal blocks of H will contain the observation dynamics for the survey and for fishing, while the off-diagonal blocks will be zero. Given these modifications, all the algorithms described previously in this paper can be used to derive estimates for this situation.

Research or other surveys of the fishery usually occur less frequently than does commercial fishing, causing part of the vector $y(t)$ to be missing at given times periods. Shumway and Stoffer (1982a) and Shumway (1988) gave a straightforward modification of the Kalman filter for this case.

DISCUSSION

I have introduced a new method for estimating population sizes from catch-at-age data that includes, if additive errors can be assumed, many of the previous difference equation models. I show that it is incorrect to treat the unobserved population sizes as parameters to be estimated rather than as missing data. I also show that the minimum mean square estimates of the population sizes are the smoothed estimates rather than the predicted estimates suggested in many papers. The model assumes neither equal variances in the errors in the population dynamics nor in the observation errors and does not require that the errors be uncorrelated. For Pacific mackerel, the smoothed estimates are shown to be much more variable than the predicted estimates.

I also suggest a new parameterization for the age-specific exploitation rate $q(a,t)$. If it is assumed that $q(a,t) = s(a)f(t)$, then the model is over determined. I put a smoothness prior on $f(t)$ in order to obtain a tradeoff between the degree of smoothness in $f(t)$ as a function of time versus fidelity to the data. The degree of differencing can be treated as a hyperparameter of the model to determine the optimal amount of differencing given the data.

An advantage of the approach of this paper is that the calculations are straightforward and simple to program, and explicit formulas are given for the optimal parameter values at each iteration of the EM algorithm. Additional optimization software is not required to perform the calculations. Moreover, properties of the Kalman filter and the EM algorithm are well known. There is a large literature giving variants of the filter to calculate sensitivity to model misspecification, and recursive formulas for the derivatives with respect to a given parameter of the model also exist in the literature.

It is also simple to include environmental variables into the formulation, either as additional state variables or as fixed effects in the observation equation or both (see Sallas and Harville [1988] on how to estimate the fixed effect parameters within the context of Kalman filtering). Thus the influence of the environment can be modeled directly, rather than resorting to the conventional practice of obtaining population estimates first and correlating these estimates with the environmental variables second.

A disadvantage of my approach is that there is no guarantee that any of the estimates of the underlying population sizes will be positive. The population sizes are treated as normal random variables, and it is quite possible for the additive corrections in the filtered or smoothed estimates to make small population sizes negative if the observation error is large. P. Sullivan (fn. 3) has found that for a length-based model the Kalman filtering approach works best when there are pulses in the recruitment, that is, when the population is not in equilibrium. The likelihood surface is such that without recruitment pulses it is difficult to estimate the parameters of the growth-curve. Most fisheries are not in equilibrium, however. As the models in this paper do not contain a growth-curve, it is unclear if a similar finding will be valid.

Some of my results suggest that the estimates are sensitive to the form of the model chosen for the population dynamics. This is not surprising, because, unlike most missing data problems, the missing part of the data is never observed directly, but only through the presumed form of the dynamics. For example, when modeling catch (or catch per unit effort) against an environmental variable, catch data often are not available for all periods. But there are at least some periods when both variables are observed, which can be used to estimate the relationship between the two sets of variables. This relationship is used to produce the smoothed estimates of the missing data. For estimating population sizes from catch-at-age data, the a priori estimate of the form of the observation equation replaces this empirically derived estimate.

In many of the references cited, multiplicative errors are preferred in the observation equation because variances appear to change with the size of the population. My experience is that relaxing the assumption of equal, uncorrelated errors appears to at least partially take into account the observed differences. If the model estimates are not satisfactory, assuming additive, gaussian errors, then the regular EM algorithm can be used to properly estimate the smoothed estimates of the underlying population. However, the EM algorithm requires the complete data likelihood as well as the expectation of the log-likelihood with respect to $(y(1), \ldots, y(T))$. In multiplicative models, assumptions about the error structure can lead to very complicated multivariate distributions for the complete data due to the Jacobian of the transformation. The conditional expectation of the log-likelihood may have to be evaluated by numerically integrating a nontrivial multiple integral. Certainly, as a first pass, the simpler techniques of this paper would appear to have a lot to offer as an alternative.

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STATUS OF THE WASHINGTON-OREGON-CALIFORNIA SABLEFISH STOCK IN 1988

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Abstract

The west coast sablefish stock is modeled in two stages. The first stage is a synthesis model simultaneously fit to the time series of catch biomass by trawl and fixed gear, the size and age composition of these fisheries components in 1986 and 1987, the time series of relative abundance of middle aged sablefish as measured by the northern and southern pot indexes, the recruitment information in the tri-ennial trawl surveys, and the exploitation rate information in the tag return data. In addition to estimating the time series of abundance and mortality for the sablefish, the model provides new insights on sablefish growth and of the influence the sampling process has on our perception of growth. The mean total biomass during 1988 was 94,700 mt and the age 3+ biomass was 78,600 mt. The biomass levels at the beginning of the year were 107,500 and 89,600 mt, respectively. The total F imposed by a 10,800 mt fishery in 1988 will be 0.15. Plausible, but less likely, alternative models that either emphasize the fit to the pot survey time series or de-emphasize the fit to the age composition data produce lower estimates of current stock abundance.

The second stage of the modeling process estimates the stock productivity at equilibrium and makes short-term yield forecasts utilizing a dynamic pool model and output of the synthesis model. The dynamic pool model is driven by either a Beverton-Holt stock-recruitment function or constant recruitment. Given the early age at recruitment to the fishery relative to the age at first maturity, the spawning biomass is reduced to only about 25% of the virgin level, so utilization of the B-H recruitment function seems prudent. If a 52:48 trawl:fixed gear allocation is maintained in the future, then the MSY for this stock is 8,200 mt at a mean age 3+ biomass of 67,800 mt and a F[MSY] equal to 0.13. An ABC in 1989 of 9,000 mt is indicated by applying the F[MSY] to the current stock structure. At this exploitation rateand if there are no great deviations in recruitment, the stock would be near the biomass yielding MSY in about 20 years and the ABC would then be reduced to about 8200 mt. At F = 0.15 the ABC in 1989 would be 10,400 mt and the population would reach the MSY level in about 1995.

Introduction

The fishery for sablefish, Anoplopoma fimbria, along the coasts of Washington, Oregon, and California has landed approximately 13,000 mt per year since 1981. Its landed value of approximately $11 million makes it the most valuable single species in the west coast groundfish fishery. Recent landings have been composed of 52% by trawlers and 48% by fixed gear (primarily pots and long-line). Management of the fishery includes a size limit of 22 inches total length (53 cm fork length) enacted in 1983, and an annual quota. The quota for the 1988 fishery was reduced to 10,000 mt due to concerns that the stock was in danger of being over-fished. For the first time, the 1988 quota was allocated to trawl and fixed gear according to the recent 52:48 ratio of their landings.

The annual quota for sablefish, and most other west coast groundfish species, is set on the basis of current exploitable biomass and the fishing mortality rate at maximum sustainable yield (and $F_{0.1}$). Past analyses have not been able to unambiguously estimate these two quantities because of great inadequacies in the sablefish database. Here we develop a sophisticated model with which to integrate information from diverse data sources and to make synthetic estimates of historical abundance and mortality for the west coast sablefish stock.

Assessment Philosophy and Basic Model Structure

If the sablefish database was lengthy, precise, and well-defined we could conduct a conventional assessment via cohort analysis. Alternatively, if we had one accurate, precise survey and accurate estimates of growth and natural mortality we could try stock reduction analysis, a simpler, non-age structured model. Unfortunately, the sablefish database is scanty and diverse, and none of the observations measure what we most need to know - the total fishable biomass. The measured quantities do, however, put constraints on the fishable biomass, but to make use of these data our assessment must make explicit definition of the relation between what has been measured and what we estimate to be in the population.

The assessment is a synthesis of a separable catch-at-age analysis with two types of fisheries (trawl and fixed) and 2 years of fishery data, and the following auxiliary information: recruitments in 80, 83, and 86 were observed by the tri-ennial trawl surveys, a time series of relative abundance of some middle age/size range has been observed by the pot index surveys, and the time series of fishing mortality should be consistent with the pattern of tag returns. Thus, information on the absolute level of abundance comes from the recruitment surveys and natural mortality, and and from the tag returns which set the magnitude of the exploitation rate. Estimation of the age specific pattern of availability to the tri-ennial trawl survey, to the northern and southern pot surveys, and to the fixed and trawl fisheries is most difficult because of the scarcity of age composition data and because of the high variability in the existing age composition data.

Methot (1986, 1988), following Fournier and Archibald (1982), developed a model in which the estimated sampled age composition is smeared by some estimated level of ageing error before being compared to observed age compositions. This smearing of true ages to observed ages is entirely analagous to the conversion of age to length, then conducting the goodness of fit in terms of length compositions. Because of the much greater availability of sablefish length composition data, we utilize the following strategy for its assessment. In each time period, the estimate of population numbers at age is converted to an estimate of the population length composition via an estimated growth curve and variance in length at age. Estimates of length-specific selectivity are then used to calculate the estimated length composition in each type of sample (e.g. trawl survey, pot survey, fixed and trawl fishery). Equivalent age-specific selectivities must still be calculated in order to calculate age-specific fishing mortalities. Age-specific selectivities are calculated by weighting length-specific selectivities with distributions of length at age. Because large and small fish at a given age usually have different selectivities, the mean size at age observed in a particular type of sample will be a biased estimate of the population mean size at age. The above scheme allows calculation of the magnitude of the bias and for calculation of the appropriate mean size at age. Goodness of fit to the entire sablefish database is evaluated by calculation of the log likelihood for each type of data, then summing these into an overall log likelihood. The parameters which define the length-specific selectivities and the recruitments are iteratively adjusted to maximize the overall log likelihood function.

The following sections define the sablefish database, various auxiliary inputs to the model, then define the model in more detail. The synthesis model will be used to determine the current status of the sablefish stock. Model output will be used as input to a dynamic pool model for determination of equilibrium and short-term yields under a variety of quota management strategies.

Data

Area and Time

The region to be modeled is bounded on the south by the U.S.-Mexico border and on the north by the U.S.-Canada border, and is described as the west coast (Figure 1). There is little catch and scant survey data south of Monterey Bay, and even less catch and data south of Pt. Conception. The specification of the northern boundary is important because sablefish are abundant throughout this region and the fishery operates near and on both sides of the border. Although some tagged sablefish have crossed this border, two observations suggest that the interchange is limited in this area. First, the size distribution of sablefish captured at the northernmost pot index site (Nitinat Canyon) off northern Washington is much larger than that of sablefish captured at southern sites and is more similar to the large fish found off British Columbia (Parks and Shaw, 1988). Second, the 1977 yearclass was extraordinarily abundant off Canada (McFarlane and Beamish, 1983a) and throughout Alaskan waters, but was not at all exceptional along the west coast according to the age composition in the 1983 and 1985 pot index surveys (Parks and Shaw, 1987).

The time series to be analyzed begins in 1970 and extends through 1987. Landings during the period 1956-1970 (Figure 2) averaged 3512 metric tons (mt) and the west coast stock is assumed to be in equilibrium with this catch level in 1970. Most types of survey data begin in 1979, but a precursor to the northern pot index was conducted in 1971[1/] and this observation is included in the analysis. An estimate of the 1988 landings is included to obtain a better estimate of recent trends in fishing mortality.

The model is run on an annual basis using calendar years. Recruitment is defined to occur at age 1 on January 1, although these recruits are barely available to the fixed gear fisheries and the pot surveys. Fishing mortality is implicitly assumed to be constant throughout the year. Surveys are typically conducted in July - October and are assumed here to represent the mean abundance of sablefish within the calendar year.

Catch

Landings for the period 1956 - 1987 were categorized by INPFC area and by gear type (Lynde 1986; PacFIN data series 1981-1987). The four gear types are longline, pot, trawl and miscellaneous. Shrimp trawl landings are included in trawl, set net landings are included in miscellaneous. Foreign landings were allocated to the following gear types: Japan to longline, USSR to trawl, Poland to trawl, Korea to pot, and other to miscellaneous. Landings from the Vancouver INPFC area were processed to delete the Canadian domestic landings (PMFC areas 3D and 3CCN). The PMFC area for other foreign landings in the Vancouver INPFC region is unknown, so these other foreign landings are included in the total landings for the U.S. Vancouver region. Landings from all west coast INPFC regions (Conception - U.S. Vancouver) were summed for analysis here

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[1] Shippen (1972) Progress report on sablefish (blackcod) studies by the United States National Marine Fisheries Service, 1971-1972. Int. N. Pac. Fish. Comm. Docu. Serial No. 1508.

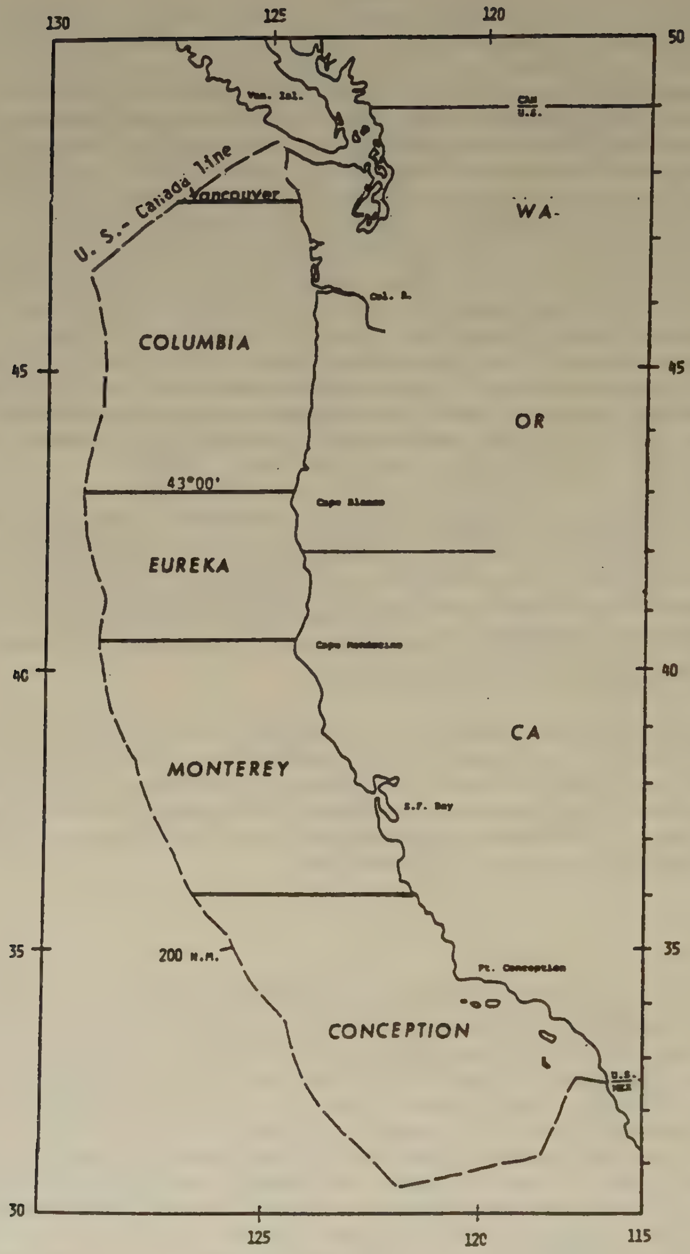

130
125
120
50
45
40
35
30
125
120
115
Van. Isl.
CAN
U.S.
U. S. - Canada line
Vancouver
WA
Col. R.
COLUMBIA
OR
43°00'
Cape Blanco
EUREKA
Cape Mendocino
CA
MONTEREY
S.F. Bay
200 N.M.
Pt. Conception
CONCEPTION
U.S.
MEX

Figure 1. INPFC statistical areas in the U.S. EEZ seaward of Washington, Oregon, and California.

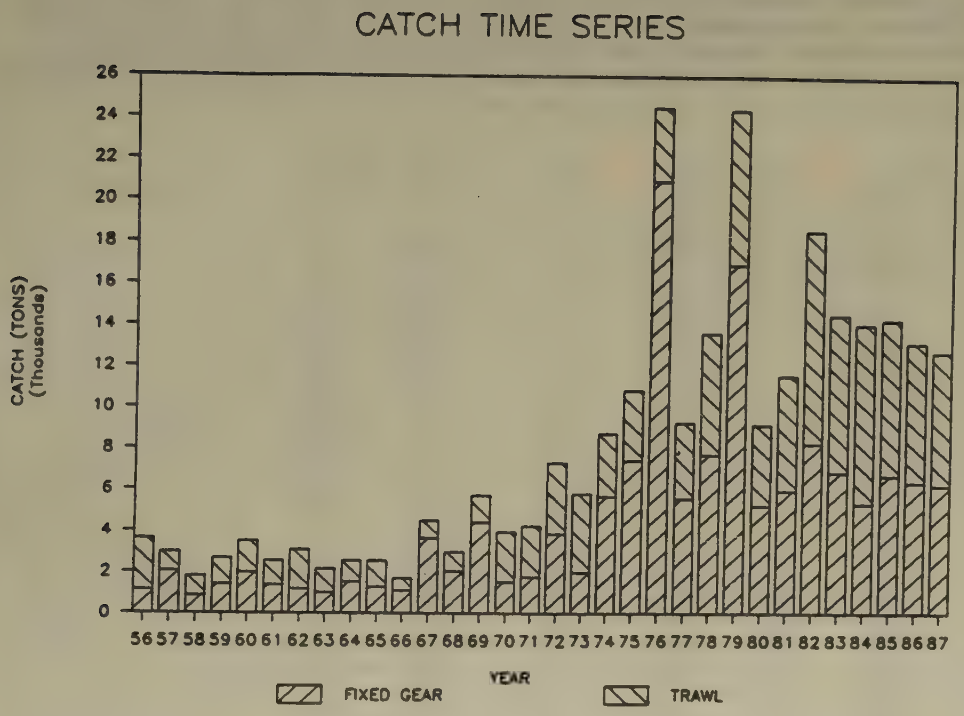


Figure 2. Sablefish catch time series showing proportion by trawl and by fixed gear.

Table 1. Landings of sablefish along the California, Oregon, Washington coast. Includes catches by foreign fishing vessels in this region and catches by non-Canadian foreign vessels throughout the Vancouver INPFC region. Catch by foreign vessels was assigned to a characteristic gear type (see text). Catch by miscellaneous gear was assigned proportionally to fixed and trawl gear categories. Catches for 1988 were estimated to allow running the model forward one year.

					- Condensed -	
Year	LLine	Pot	Trawl	Misc	Fixed	Trawl
56	1129	0	2477	7	1131	2482
57	2051	0	914	1	2051	914
58	855	0	948	0	855	948
59	1398	0	1273	1	1398	1273
60	1980	0	1510	0	1980	1510
61	1121	0	935	482	1384	1154
62	1100	0	1794	163	1162	1895
63	931	0	1053	157	1005	1136
64	1341	0	922	299	1519	1043
65	1018	0	1023	493	1264	1270
66	789	0	427	474	1097	593
67	3341	0	795	372	3641	867
68	1787	0	815	365	2038	929
69	4087	0	1186	432	4422	1283
70	1391	114	2395	41	1521	2420
71	1511	193	2395	138	1761	2475
72	3492	355	3435	37	3866	3453
73	1124	863	3791	28	1997	3809
74	2439	3240	3044	13	5687	3048
75	1736	5689	3391	8	7431	3393
76	1219	19725	3553	22	20962	3556
77	1441	4140	3662	7	5585	3665
78	1709	5753	5748	405	7691	5924
79	4187	12333	7252	601	16939	7435
80	1378	3632	3721	416	5248	3898
81	1925	3896	5437	294	5973	5579
82	1626	6494	10158	314	8259	10333
83	1003	5399	7154	963	6857	7662
84	1022	3822	7933	1296	5335	8738
85	2753	3637	7198	707	6722	7573
86	3576	2115	6024	1470	6405	6780
87	4187	2031	6463	32	6234	6479
88	0	0	0	0	4800	5200

(Table 1). The few miscellaneous landings were allocated proportionally to longline, pot and trawl gear types.

A port sampling program initiated in 1986 provides age and length composition data, by sex, for each major gear type in the west coast sablefish fishery (Appendix tables 1,2). Size compositions in the longline and pot fisheries are similar (Figure 3,4,5) and, in preliminary runs of the model, their estimated selectivity patterns were similar. Therefore, longline and pot landings, age composition, and length composition were combined into one fixed gear category.

Trawl Surveys

Bottom trawl surveys were conducted between Monterey Bay and Vancouver Island in the 30-200 fathom depth zone during 1980, 1983, 1986 and in the 50-250 fathom zone in 1977 (e.g. Coleman, 1986; Weinberg et al., 1984). Depth-specific trends in sablefish mean size complicate any attempt to extrapolate these nearshore surveys to an estimate of total population biomass. However, analyzing these data as estimates of age 1 recruit abundance is realistic. The size frequency distributions for each survey indicate a distinct mode at 38-39 cm FL (Figure 6); these are the age 1 fish. Age 0 fish seem to be about 26 cm and are rarely taken. When the data from all four surveys are combined and stratified by 10 fathom depth intervals (Table 2) the following patterns emerge. Where the bottom depth is less than 80 fathoms the catch is nearly 100% small (<42cm, i.e. age 1) sablefish. This size group is nearly non-existent in tows taken at depths greater than 150 fathoms. The mean catch in the 40-49 fathom zone is 48 sablefish per tow (N tows = 214), which is the greatest catch rate among all the 10 fathom intervals between 30 and 200 fathoms. The mean catch in the 30-39 fathom zone is only 2 sablefish per tow (N tows = 168). We conclude that most age 1 sablefish are found between 40 and 150 fathoms, and that a survey which covers the depth range 30-200 fathoms includes nearly 100% of the age 1 fish, and can be used as a quantitative assessment of their abundance. The 1977 survey did not work nearshore of 50 fathoms so cannot be used as a comparable survey. Calibration of the 1977 survey is not possible because the <50 fathom depth zone contained a highly variable portion of the total abundance in the other surveys.

The northern extent of the 1986 survey was the U.S.-Canada border, and the 1980 and 1983 surveys worked further north to latitude 49°15'. The 1980 and 1983 survey results were processed to delete samples taken north of the U.S.-Canada border. The southern extent of all surveys was Monterey Bay. The bottom area between Monterey Bay, the U.S.-Canada border, and the 30 and 200 fathom isobaths is approximately 11600 nm . One may consider extrapolating the survey results southward. Extrapolation to Pt. Conception would increase the area to about 12350 nm , a 6.5% increase. Extrapolation to the U.S.-Mexico border would increase the area to 14550 nm , a 25% increase. Any extrapolation requires the assumption that the density of sablefish in the 30-200 fathom depth zone is the same north and south of Monterey Bay. No extrapolation was made in the preliminary analysis and, in the final analysis, the trawl survey abundances were extrapolated to Pt. Conception.

The synthesis model separately examines the total numbers observed in the survey, the males' size composition, and the females' size composition. Total population numbers (Table 3) were taken directly from the output of the RACE

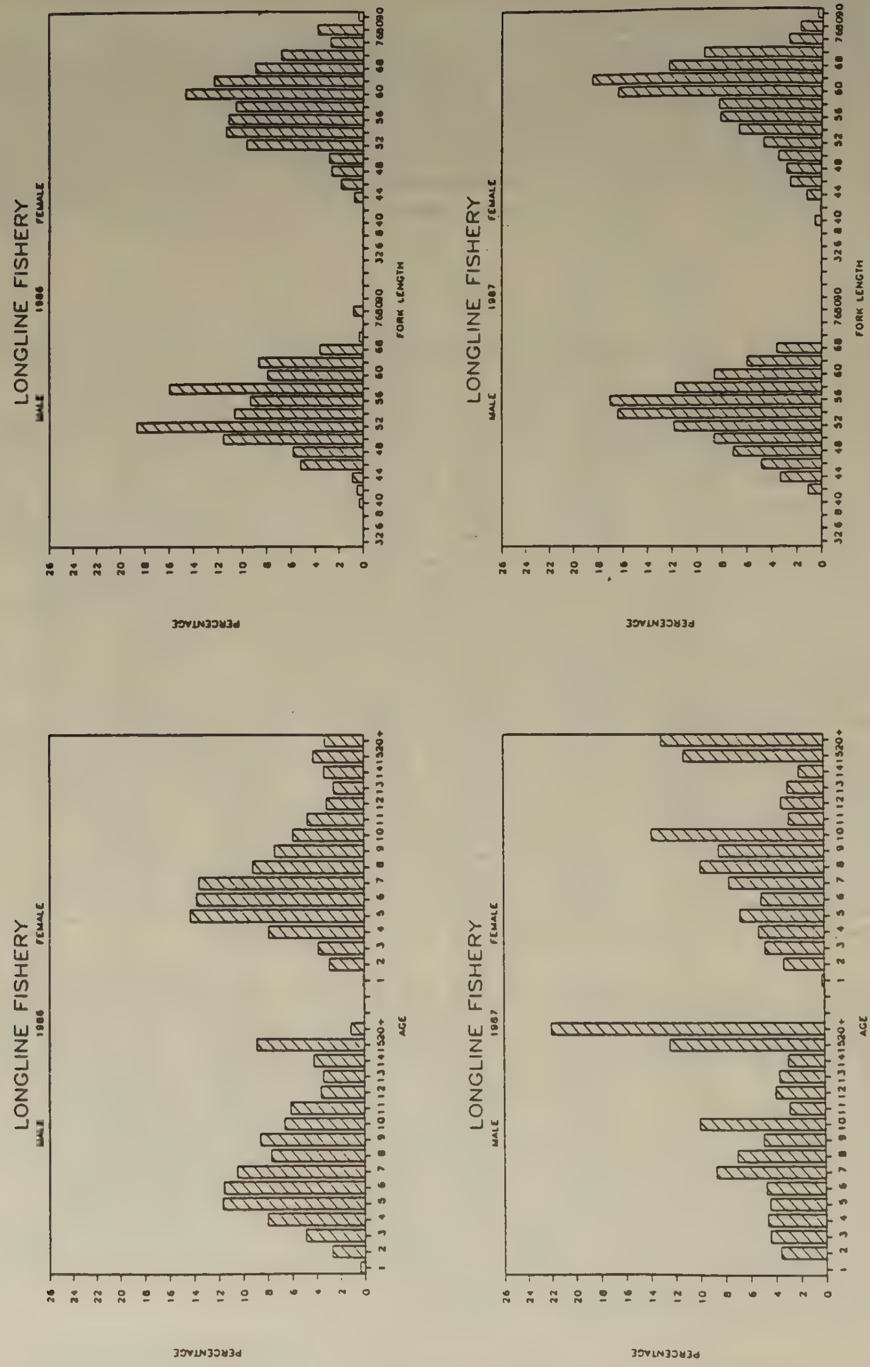


Figure 3. Size and age frequencies in the 1986 and 1987 longline fishery.

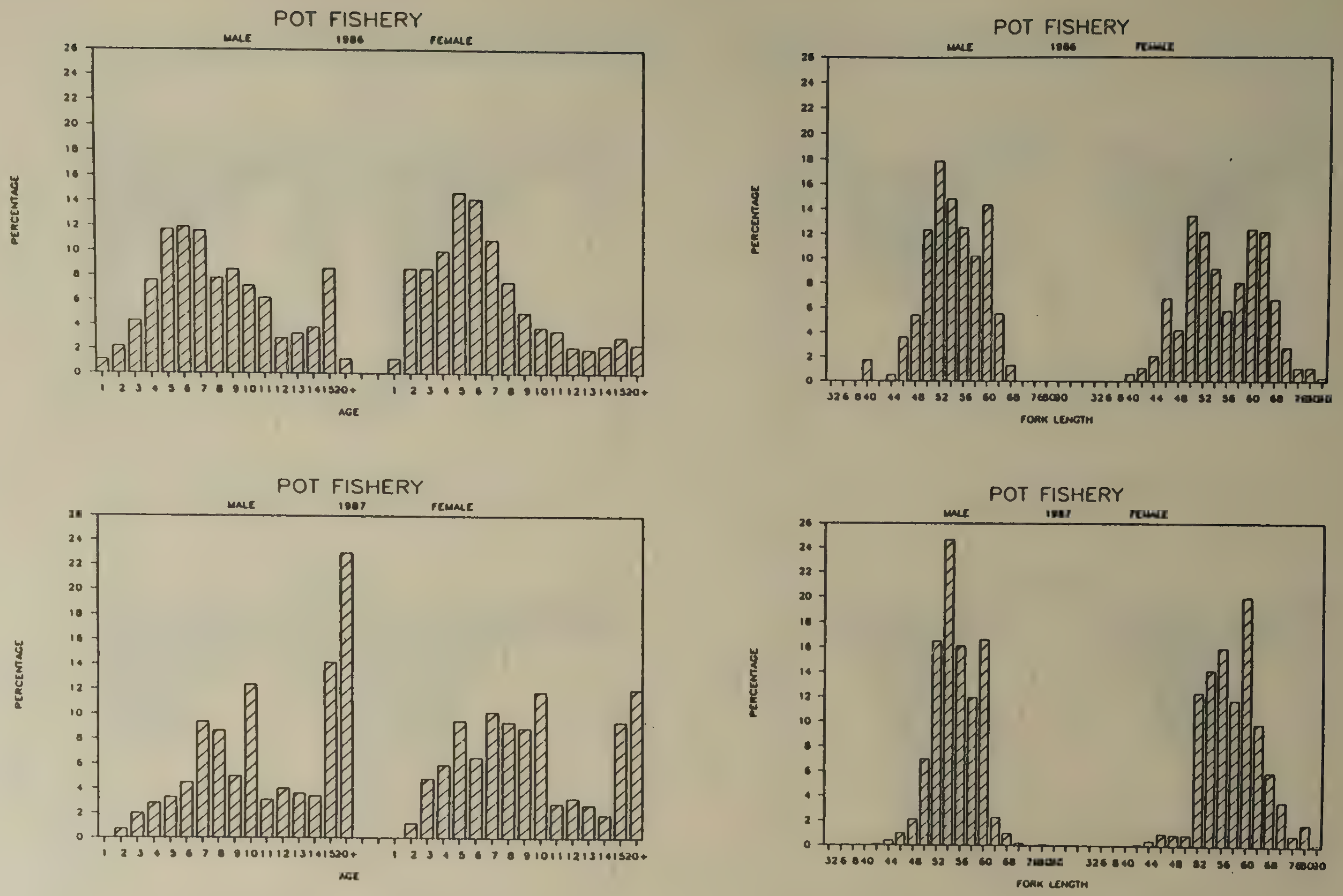


Figure 4. Size and age frequencies in the 1986 and 1987 pot fishery.

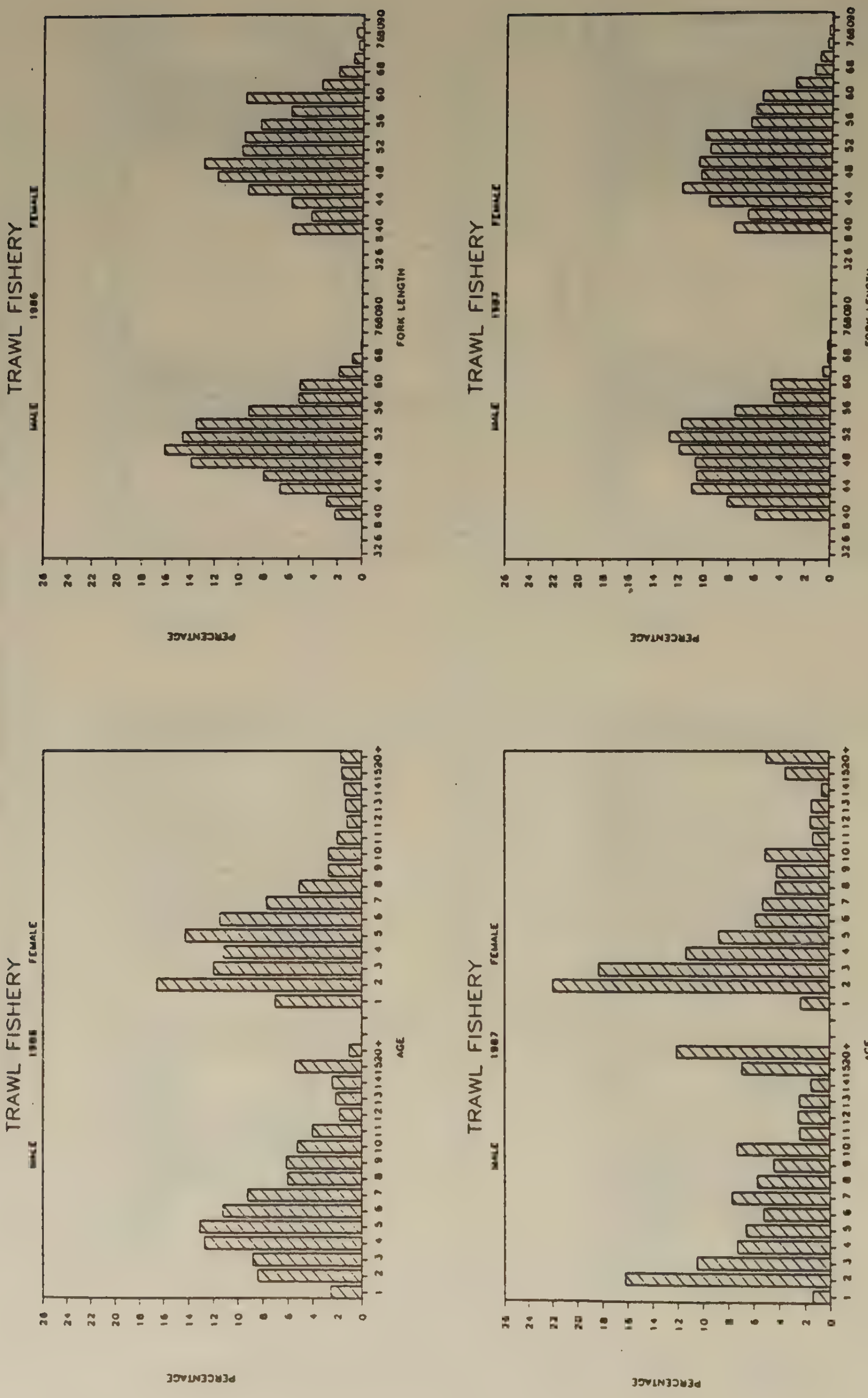


Figure 5. Size and age frequencies in the 1986 and 1987 trawl fishery.

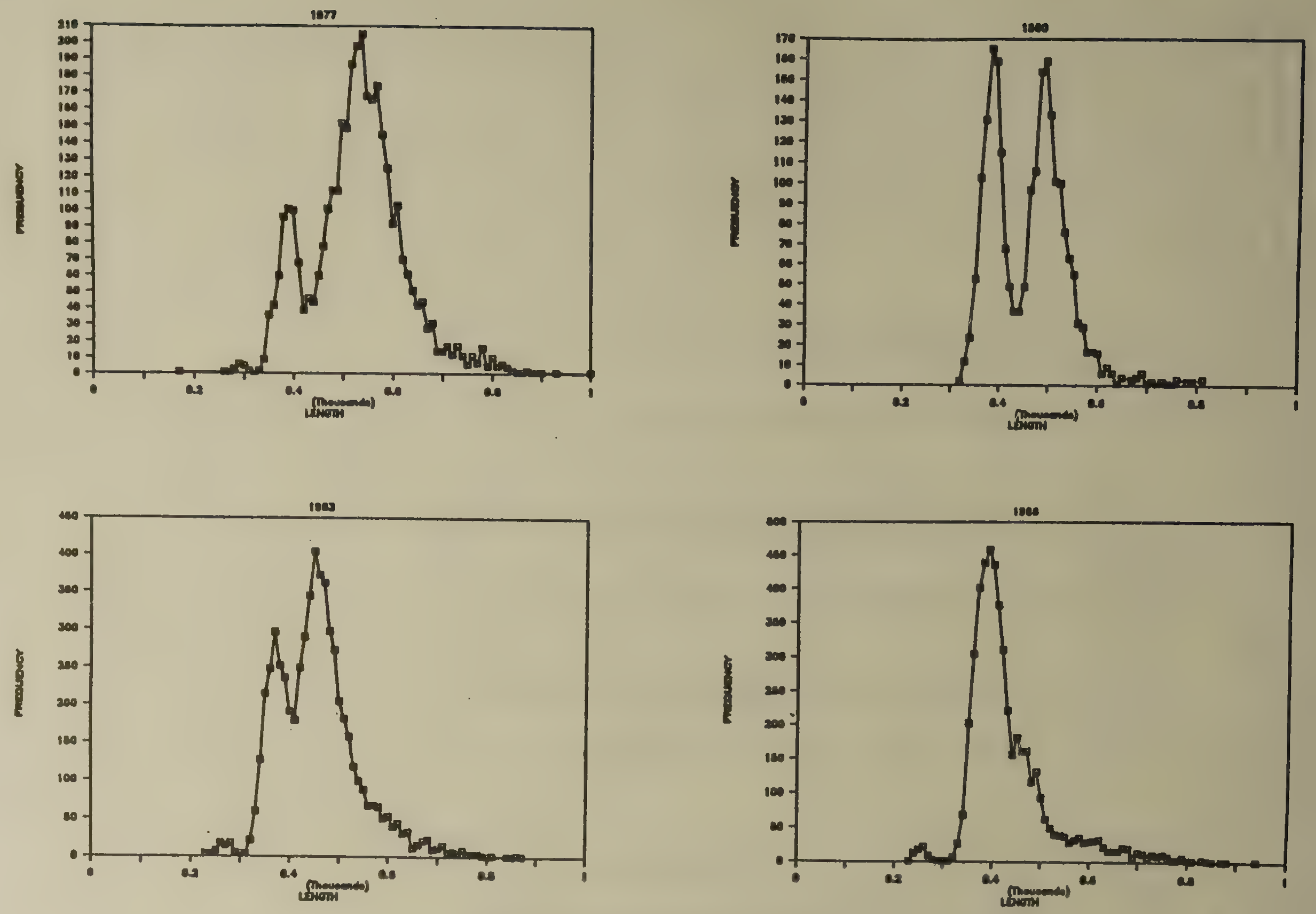


Figure 6. Unweighted size frequencies in the nearshore tri-ennial trawl surveys, sexes are combined.

Table 2. Statistics on depth distribution in trawl surveys. N is the total number of trawls in the four surveys (1977, 1980, 1983, and 1986); % zero is the percentage with no sablefish; The statistics on number of sablefish are simply based on number per tow; for the categories under % <42cm, N is the number of tows for which the number of measured sablefish was at least 5 and, for these tows, % is the percentage of the measured sablefish which were less than 42 cm fork length.

	Trawls		Number of sablefish				% <42 cm	
Depth	N	%zero	Mean	S.D.	Median	Max	N	%
30-39	168	74%	2	17	0	217	4	100%
40-	214	59	48	408	0	4473	12	88
50-	289	54	15	69	0	740	31	71
60-	312	40	25	152	1	1892	43	65
70-	262	34	27	183	2	2332	36	46
80-	184	30	26	202	3	2731	31	32
90-	136	17	27	88	5	752	30	26
100-	101	6	19	37	7	248	26	22
110-	115	18	18	50	4	468	26	18
120-	87	26	16	48	3	379	19	17
130-	53	38	16	41	3	266	13	11
140-	49	27	24	100	5	699	11	6
150-	51	12	17	30	7	172	15	12
160-	50	16	18	30	5	153	17	0
170-	55	22	25	78	6	555	18	2
180-	52	33	16	30	2	143	11	5
190-	24	21	10	10	8	40	6	1
200-	20	|	17	32	5	141	6	1
210-	21	|	11	13	5	45	6	0
220-	28	|	8	9	6	42	7	4
230-	29	17	8	10	4	38	9	4
240-	22	|	8	9	5	30	9	5
250-	7	|	18	37	7	101	2	8

Table 3. Survey observations of sablefish abundance. Trawl values are in thousands of fish. Pot values are in fish per pot. The cv for the small fish component of the trawl survey is assumed to be the same as the calculated cv for the entire size range, but these small fish cv values will have no effect on the model.

	Tri-ennial Trawl							
Year	<42 cm		All		N Pot		S Pot	
	value	cv	value	cv	value	cv	value	cv
71	—		—		10.30	.245	—	
72	—		—		—		—	
73	—		—		—		—	
74	—		—		—		—	
75	—		—		—		—	
76	—		—		—		—	
77	—		—		—		—	
78	—		—		—		—	
79	—		—		11.40	.316	—	
80	32253	.461	50158	.461	6.80	.124	—	
81	—		—		4.80	.200	—	
82	—		—		—		—	
83	16875	.368	38097	.368	10.60	.092	—	
84	—		—		—		9.80	.108
85	—		—		7.40	.193	—	
86	19267	.264	28973	.264	—		4.60	.096
87	—		—		2.80	.189	—	

BIOMASS program. Male and female size compositions could not be used directly from this output because they do not include the substantial numbers of small unsexed fish. Instead the estimated size composition for combined sexes was split into a male and female component (Figure 7) based on the estimated sex ratio within each length category.

The selectivity function which defines the relation between the true population and the population surveyed by the nearshore trawl survey should be strongly peaked at the size range which represents age 1 sablefish. It is expected that the model will be able to estimate the shape of this function from the size distribution data in these 3 surveys. The model treats the total survey numbers as a quantitative estimate of the abundance of a subset of the population; that subset being defined by the estimated selectivity function. Preliminary runs of the model disclosed an ambiguity in this definition: the model could improve the fit to the observed total survey numbers by either adjusting the estimated numbers of fish in the population, or by adjusting the selectivity function that defined the proportion of each size that contributed to the total survey numbers (subject to the constraint that at least one size category had selectivity equal to 1.0). If the model took the latter approach, it could degrade the fit to the survey size compositions. Thus, the relative emphasis placed on fitting the survey abundances and the survey size compositions became critical. We adopted the following alternative approach to alleviate this problem. A fixed subset of the trawl survey, those sablefish <42 cm, were defined to be 100% available to the survey. This size group includes nearly all of the age 1 fish and few fish of other ages. The model then includes two versions of the trawl survey numbers (Figure 8). The first, trawl survey (all), includes the entire size range, is not considered quantitative, and a size-specific selectivity function is estimated. The second, trawl survey (small), includes only the <42 cm size range, is considered quantitative, and all sizes less than 42 cm are defined to be fully available.

Pot Surveys

In the Oregon-Washington region, surveys occurred in 1979, 80, 81, 83, 85 and 1987 (Table 3, Figure 9). Each sampled the standard depths: 150, 225, 300, 375, and 450 fathoms. Extra depths sampled in later years tend to catch larger fish and have not been included in the standard index (Parks and Shaw, 1988). Only catches from the first two sets at each site were included in the index. The sampling gear was changed in 1985 from rectangular traps to conical traps. The conical traps are more efficient, and the historical catches from rectangular traps have been adjusted upwards by a measured calibration factor of 1.408 (Parks and Shaw, 1987). The gear type had no effect on the size composition of the catch. Also in 1985 the number of sites was increased from 4 to 8. The mean index was relatively unaffected (7.6 for old sites and 7.3 for new sites in 1985, 3.1 and 2.5 in 1987).

In 1971 a precursor to the northern pot index was conducted at 3 of the sites that eventually were included in the northern pot index[1/]. The gear (rectangular trap) and depths (150-450 fathoms) were identical to that used in 1979. We consider this cruise to be a valid northern pot index observation.

In the California - southern Oregon region, surveys occurred in 1984 and 1986 with 9 sites occupied in each year. The depth range is 225 - 525 fathoms. This is 75 fathoms deeper than the northern index depth range so we expect to

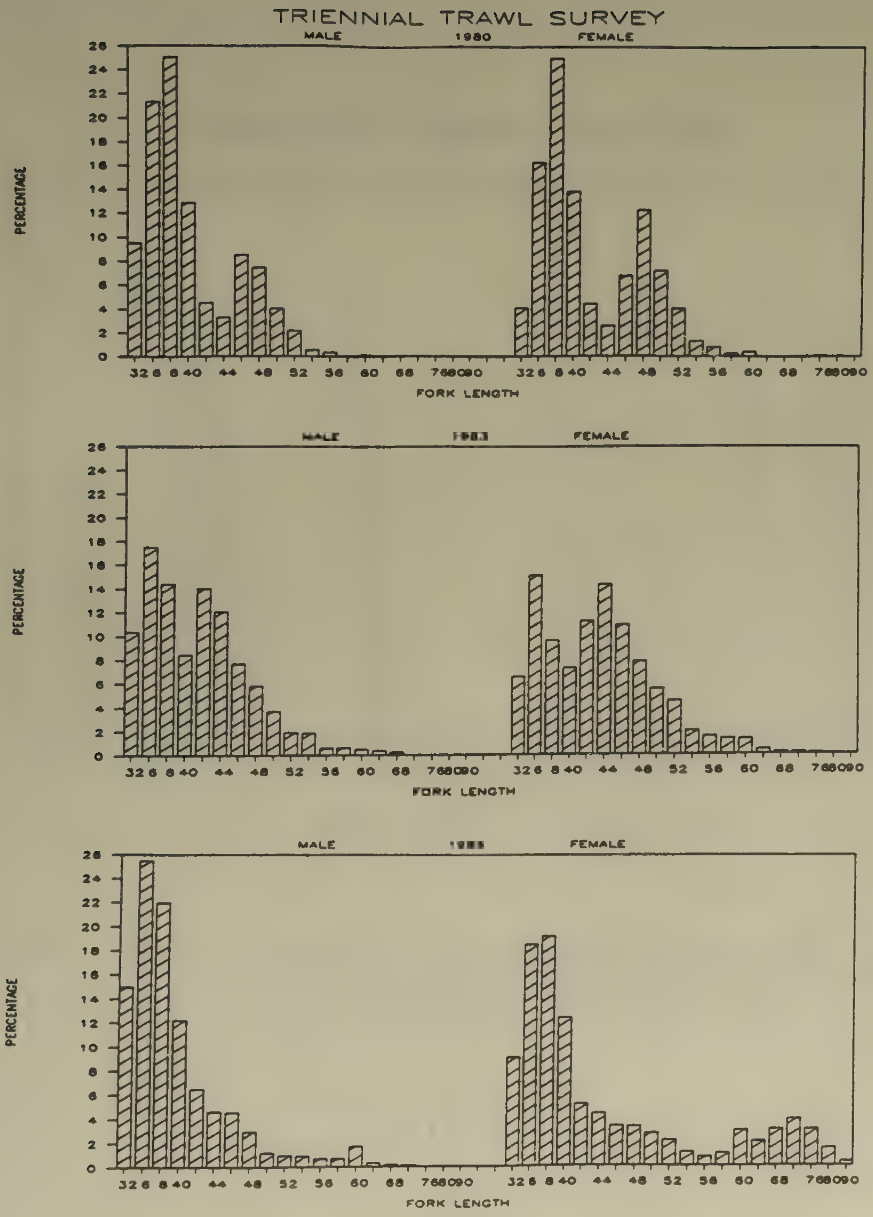


Figure 7. Condensed size frequencies in the trawl surveys by sex and weighted by catch rates. Size categories are 32-35 cm, then by 2 cm to 60 cm, by 4 cm to 80 cm, and by 10 cm to 100 cm.

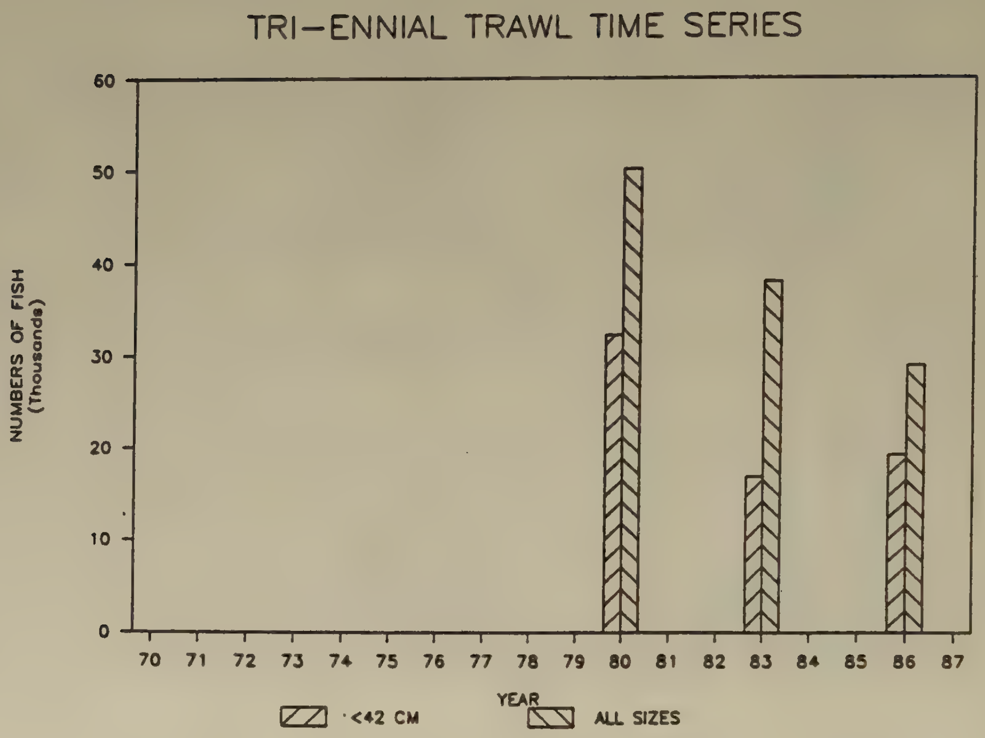


Figure 8. Trawl survey time series showing the numbers of small (<42 cm) sablefish and the numbers for the entire size range.

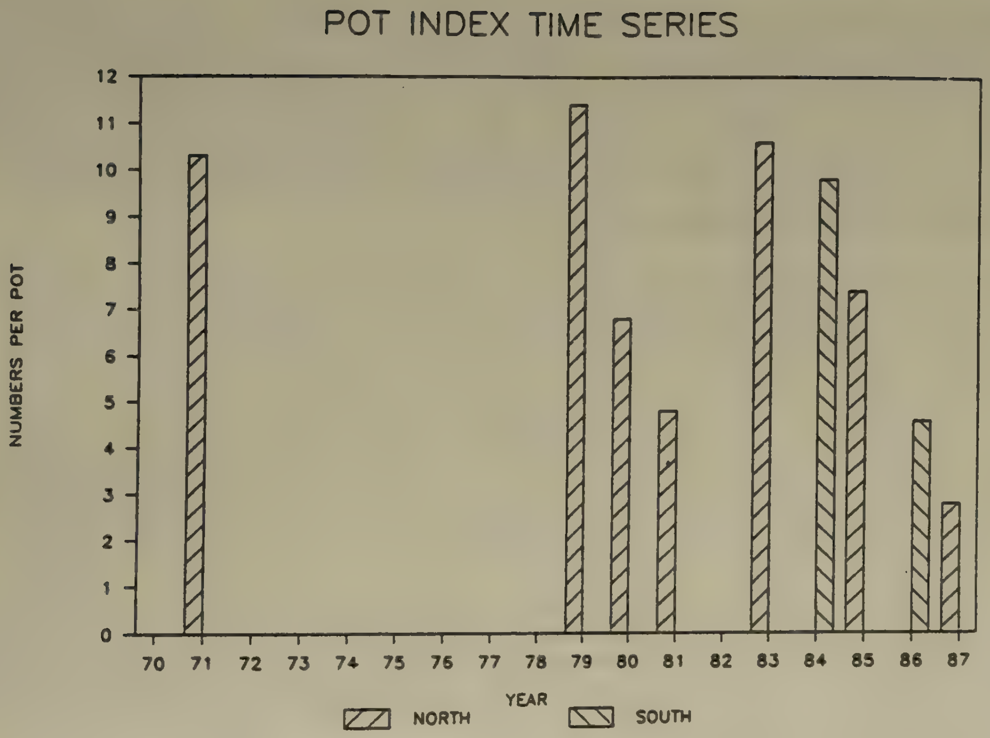


Figure 9. Northern and southern pot survey time series.

observe fewer small fish in the south index area. However, this tendency may be countered by the tendency for larger/older fish to be more common in the north. Separate selectivity functions will be estimated for the northern and southern pot surveys.

Variance estimates for recent pot index surveys have been calculated under the assumption of fixed site effects (Parks and Shaw, 1988). Because these analyses do not simultaneously analyze all survey years (thus obtaining a site effect averaged over all years), and because earlier work (Kimura and Balsiger, 1985) determined appropriate sample size on the basis of random site effects, we have recalculated the survey variances. Here we calculate a standard error for each survey from the standard deviation of the individual site values within each year (Table 3). These values are typically larger than those calculated from the fixed effect model.

All sablefish captured in the pot surveys are measured to determine the total size composition, a random sample is examined for sex, length, and age, and many are tagged and released. The size composition by sex from each random sample should be weighted by the total numbers captured at that site/depth. Alternatively, we employ the same approach as that used to process the trawl size compositions. The random sample data are pooled and used to calculate the sex ratio in each size category. These measured sex ratios are then used to split the total size composition into male and female components based on the measured sex ratio in each length category. The length composition vector for each sex (Appendix Table 2) is then scaled so that it totals to the number of fish observed for that sex in the random samples.

Age composition data is available from the random samples for the 1983 and 1985 northern pot index surveys. The age-length key for each sex in each survey was compressed into the length categories defined below, ages 15-19 were combined, and ages 20+ were combined. The revised length compositions defined above were then multiplied by the corresponding key to obtain new estimates of the sample age composition (Appendix Table 1).

Age and Length Categories

Length compositions from all surveys and fisheries were compressed into 21 categories defined by the following lower and upper bounds of fork length:

L 0 32 36 38 40 42 44 46 48 50 52 54 56 58 60 64 68 72 76 80 90
U 31 35 37 39 41 43 45 47 49 51 53 55 57 59 63 67 71 75 79 89 100

Age compositions from all surveys and fisheries were compressed into the following categories:

1 2 3 4 5 6 7 8 9 0 11 12 13 14 15-19 20+.

The lower and upper tail of each size and age distribution was further compressed so that the first non-zero value had at least 5 observed fish.

Tag Recaptures

Sablefish have been tagged and released on the west coast beginning in about 1971 with a large release of tagged fish in 1972 (Shaw, 1984). The rate at which these tags have been returned contains information on the fishing mortality rate. Here we utilize only those tag returns from fish which were greater than 52.9 cm at the time of release, because preliminary analyses (William Lenarz, SWFC Tiburon, CA) indicate a reduced return rate for tags released on smaller fish. Only returns from the west coast fishing zone, as defined above, are included (Table 4). Returns from 1976 and earlier are excluded because of the low reporting rate by the large foreign fishery in 1976. Releases from the years 1971-1976 were grouped into one aggregate release year. The model analyzes these data by examining, for each release year, the percentage of tags that were returned in each subsequent year. Thus, initial tag loss and initial tagging mortality are unimportant, even if they vary from year to year. The level of reporting also is unimportant, but it is assumed to be constant. Long term tag loss is important, and is assumed to be 0.10 per year. Sensitivity to this value will be investigated.

Other Input

Natural Mortality

The most appropriate value for natural mortality should account for emigration from the U.S. zone and from the depth strata which is fished and surveyed, because an older fish which is not vulnerable to the fishery is effectively dead. The level of natural mortality is critical because it, more than any other factor, determines whether the observed numbers of recruits in the tri-ennial surveys can supply adequate population numbers at age to support the observed fisheries. Also, the relative selectivity of older fish is nearly inextricable from the estimate of natural mortality, i.e. the reduced occurrence of larger/older fish can be due to death, migration, or gear avoidance. We can try various levels of natural mortality to see which yields the most believable estimates of selectivity. The maximum longevity of fish observed in Canada, 55 years, suggests that M is about 0.08 (Hoenig, 1983). The maximum age for fish from the 1987 port sampling program ranged from 35 to 47 among the various otolith readers, yielding M estimates of 0.10 to 0.13. Effective M, which includes emigration, for sablefish in the US west coast zone probably is in the range 0.10 - 0.20. Dynamic pool models explored by Lenarz and Methot (unpublished data) during October 1987 indicated that M = 0.1 results in an abundant current stock which is inconsistent with the decline in the survey observations and which contains a large number of older fish. At M=0.2 the population would have barely been able to support the last decade of harvests unless the level of recruitment has been greater than the approximately 20 million age 1 fish observed in the 1980, 1983, and 1986 tri-ennial trawl surveys. Natural mortality is incorporated as a parameter so that its value can be easily changed. Initial runs will use M = 0.15 and alternatives will be explored.

The abundance of predators encountered by juvenile sablefish on the continental shelf must be greater than that encountered by adults on the slope. We consider it likely that juvenile sablefish have a greater natural mortality as

Table 4. Returns of tags released in the U.S. fishery zone on fish >52.9 cm in length, and recaptured in the U.S. fishery zone.

Release year	Returns in year: 77	78	79	80	81	82	83	84	85	86	87
71 - 76	30	38	85	16	22	32	21	7	6	3	4
77											
78											
79				26	26	20	10	9	10	2	4
80					121	104	137	26	27	32	10
81						57	27	8	16	16	4
82							23	7	6	10	3
83								5	5	2	2
84											
85											
86											54

a consequence of this differential distribution. We include the possibility of extra juvenile mortality with the following formulation:

$$M_a = M1 + M2 * e^{(1-a)}$$

where: M1 is the natural mortality of older fish, set at 0.15 in most runs.

M2 is the extra juvenile mortality. This parameter was set to 0.0 for the preliminary runs, then was estimated in the final runs.

Growth

The growth model should be constrained by two strong observations. One is the large maximum size, L_∞, of females (about 100 cm) and the other is the mean size at age 1, L_1, in the late summer-early autumn (38.4 cm) (Table 5, Figure 6). Growth models based on fishery or pot survey samples tend to miss these two constraining points because these samples are length-selective. By undersampling the small fish they overestimate mean size at age of young fish, thus underestimate the growth rate of these young fish. By undersampling the largest fish found in deeper water, growth models fit to these data may underestimate L_∞. Various L_∞ estimates are:

author	male	female
Klein 1986	71	83
McFarlane & Beamish 1983b	66	79
Parks & Shaw 1987		
1983 pot survey	58	68
1985 pot survey	68	80
Fujiwara and Hankin 1988	~60	~80

We used these values as guidance in selecting values for L for the preliminary runs. Then in the final model runs used the model itself to find the L values which provided the best fit.

Inclusion of the constraining length at age 1 is facilitated by recasting the Von Bertalanffy growth equation in terms of L_1 instead of T_0:

$$L = L_\infty + (L_1 - L\ ) * e^{(K*(1-t))}$$

$$\text{note: } T_0 = 1 + [\ln(1 - L_1/L_\infty)]/K.$$

Given the above growth model and estimates of L_1 and L , K can be estimated from the size at any intermediate age. The pot surveys will be shown to have maximum selectivity at about age 5, so the mean size at age 5, L_5, in the pot surveys of 1983 and 1985 will be used to calculate K. Preliminary model runs indicated a small bias (explained below) in the mean size at age 5 in the pot surveys (0.4 cm for males and 0.2 cm for females). These biases were taken into account when selecting the best L_5 for the final model runs.

A normal distribution of size at age is assumed, and the coefficient of variation is assumed to increase linearly with age. Variance of the age 1 distributions was estimated from the size distributions in the trawl surveys.

Table 5. Size distributions of sablefish in neashore trawl surveys. Only sizes pertinent to definition of the size distribution at age 1 are presented. The age 1 size distribution was determined by inspection of the total size distribution. The upper tail of the age 1 distribution was assumed to be a mirror image of the better defined lower tail.

	1977		1980		1983		1986		Total
Size	All	age 1	All	age 1	All	age 1	All	age 1	age 1
23 cm					4	0	1	0	
24					4	0	13	0	
25					8	0	18	0	
26	1	0			18	0	22	0	
27	1	0			15	0	9	0	
28	3	0			18	0	3	0	
29	6	0			6	0	1	0	
30	5	0			4	0	2	0	
31	2	0			4	4	1	1	5
32	1	1	2	2	22	22	7	7	32
33	2	2	12	12	60	60	27	27	101
34	9	9	24	24	128	128	69	69	230
35	36	36	53	53	216	216	203	203	508
36	42	42	103	103	249	249	305	305	699
37	60	60	131	131	297	297	402	402	890
38	96	96	165	165	253	253	439	439	953
39	101	101	159	159	237	237	458	458	955
40	100	100	115	115	192	128	436	436	779
41	68	68	68	68	180	60	376	376	572
42	39	39	49	49	250	22	311	311	421
43	46	36	37	24	291	4	222	203	267
44	44	9	37	12	345	0	157	69	90
45	60	2	49	2	404	0	182	27	31
46	78	1	97	0	373	0	162	7	8
47	101	0	106	0	362	0	162	1	1
48	112	0	154	0	298	0	117	0	0
49	112	0	159	0	273	0	132	0	0
.									
.									
.									
Total		602		919		1680		3341	6542
mean		39.02		38.36		37.03		38.99	38.40
std.dev.		2.34		2.29		2.17		2.58	2.58

Variance of size at age 20 was estimated from size at age data in the 1986 and 1987 fisheries.

We utilize the following growth parameters (Figure 10):

	L_1	L_5	L_∞	K	T_0	coefficient of variation at age 1	coefficient of variation at age 20
Preliminary:							
MALE:	38.4	52.3	70.0	.145	-4.489	.068	.0902
FEMALE:	38.4	57.3	85.0	.130	-3.622	.068	.1452
Final:							
MALE:	38.4	52.0	64.5	.184	-3.916	.068	.0902
FEMALE:	38.4	56.2	77.5	.152	-3.505	.068	.1452

Length-Weight

The length - weight relationship used here is taken from the pot survey conducted off California and Oregon in 1986:

$$W(kg) = .00000233*L(cm)^{3.364}$$

There is no apparent difference in this relationship between males and females (Phillips and Inamura, 1954; Fujiwara and Hankin[2/]; Klein, 1986).

Maturity and Fecundity

Percentage mature is assumed to follow a logistic function of length (Figure 11). The length at 50% mature was estimated by McDevitt (1987) from data in Phillips and Inamura (1954) to be approximately 67 cm. Mason et al. (1983) estimated, from data collected off Vancouver Island in 1980, that the size at 50% mature was 58.3 cm. Parks and Shaw (1983) estimated the size to be 56.3 cm off central California. Hunter (SWFC, unpubl. data) estimated that the value was about 59 cm off central California in 1987. Here we describe percentage mature as:

$$PCTMAT_a = \frac{1.0}{(1.0 + e^{(-.2491*(L_a-58.3))})}$$

Spawner-Recruitment

Here we use the same Beverton-Holt formulation (Figure 12) that has been used in other west coast assessments:

[2/] Characteristics of blackcod captured off Eureka, California by vessels belonging to the Fishermen's Marketing Association, July 1983 - August 1984. A report submitted to the Fishermen's Marketing Assoc. by Shunji Fujiwara and David Hankin, Dec. 1984.

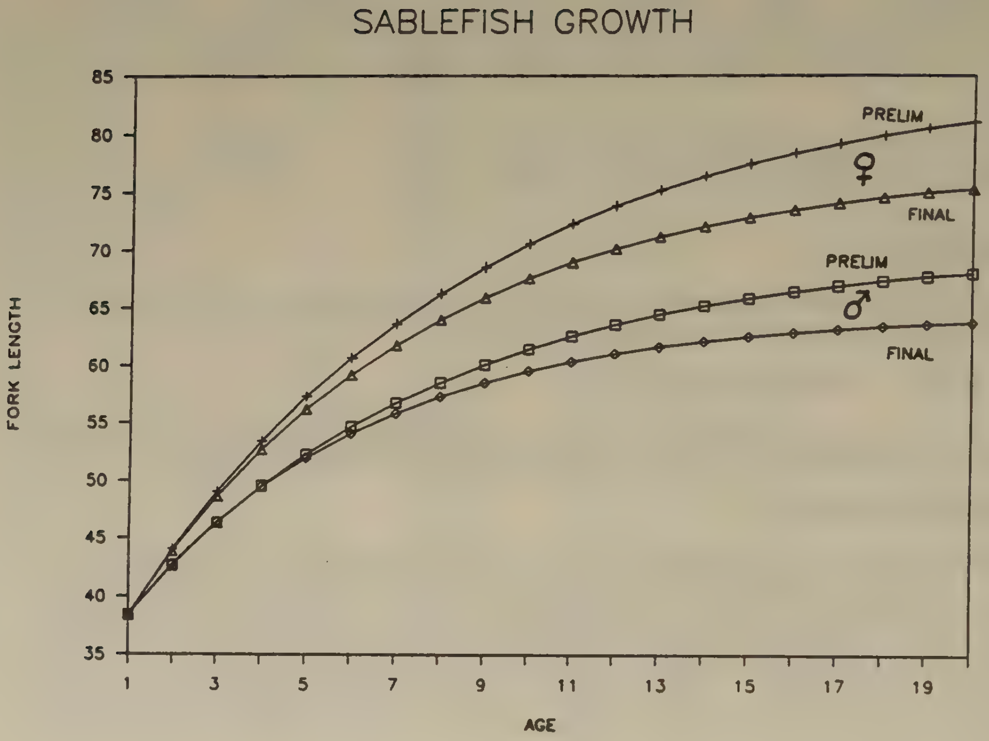


Figure 10. Growth curves for male and female sablefish using the preliminary and final parameter values.

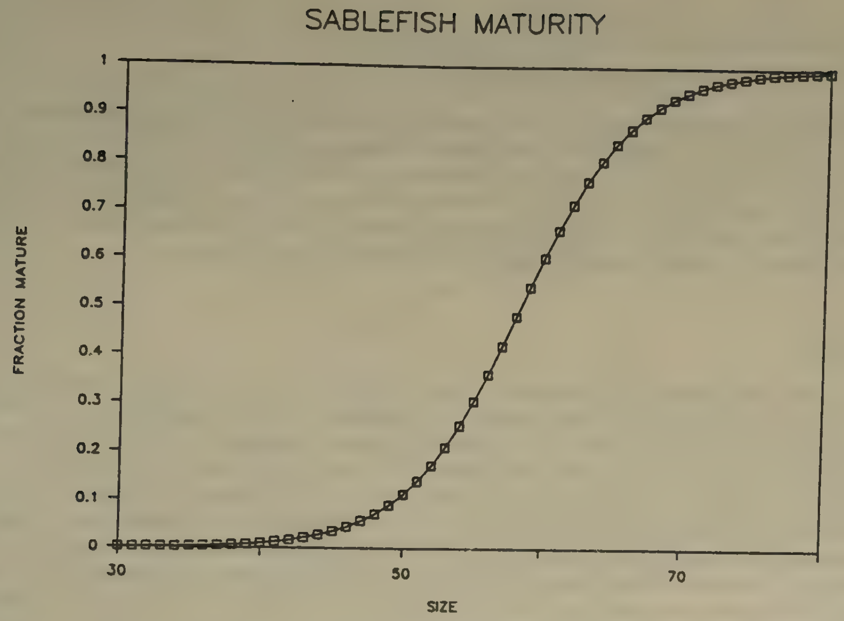


Figure 11. Percentage mature for female sablefish.

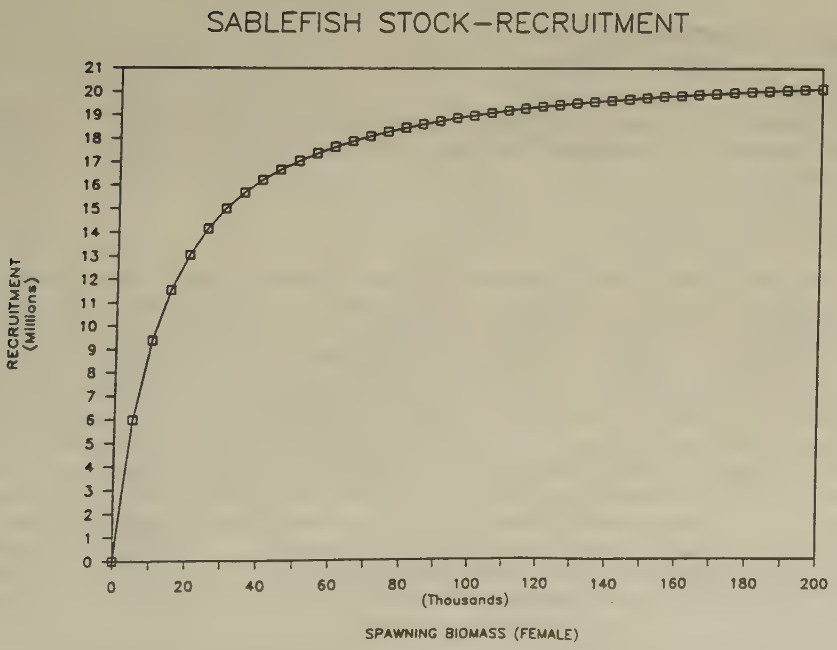


Figure 12. Spawner-recruitment relationship with DD=0.889.

$$\mathrm{RECRUIT} = \mathrm{VR} * \frac{\mathrm{SPB} / \mathrm{VSPB}}{(\ 1 - \mathrm{DD}*(1-(\mathrm{SPB}/\mathrm{VSPB}))\ )}$$

The density-dependence factor (DD) is set at 0.889 so that recruitment is 90% of virgin recruitment (VR) when spawning biomass (SPB) is 50% of virgin spawning biomass (VSPB). Spawning biomass is calculated from female numbers at age, weight at age and percentage mature at age. Virgin spawning biomass is calculated from the virgin age-structure which is calculated from the parameters which define virgin recruitment and natural mortality.

Ageing Error

Annuli in the otoliths of sablefish are difficult to interpret unambiguously, even by the break-and-burn technique. Agreement among readers is low relative to the agreement attained for otoliths of other species. Here we assume that the assigned ages are unbiased estimates of true age, but that there is substantial variability in the assigned ages. The impact of this variability is to diminish the apparent importance of abundant year classes and, especially, to enhance the apparent abundance of poor year classes. In early versions of the model, we specified the level of ageing error as a linear function of true age. When the parameters of this function were fit within the sablefish synthesis model, the estimated level of ageing error was similar to that estimated from the agreement between readers. In the final model runs we specified the standard deviation of observed age from the non-linear reader agreement function (Figure 13) fit to the 1986 fishery samples:

$$\mathrm{std.dev.}_a = \frac{A}{.223*A + 4.345}$$

We assume a normal distribution of assigned age for each true age, and generate a transition matrix, A'@A, which defines the distribution of observed age at each true age.

Trawl Discard

Discard of sablefish may occur because of poor market conditions, small size, or closed seasons. Here we attempt to incorporate one of these factors - discard in the trawl fishery due to small size. We assume that all small fish die after being captured in a trawl and discarded, and that small fish discarded from a pot or longline will survive. Inaccuracies in these two assumptions will tend to cancel each other. Length-specific data on trawl discards were obtained from two sources. Fujiwara and Hankin[2/] obtained data from the Eureka trawl fishery in 1983 and 1984. They found that the smallest size captured was 36 cm, the smallest size retained was 40 cm, and 100% retention occurred at 46 cm. A logistic function fit to their data indicates 50% retention at 42.8 cm and a slope of 1.092 (Figure 14). Pikitch (unpublished data) placed observers on board domestic fishing vessels to document levels of by-catch in 1986 and 1987. Information collected by these observers can also be used to calculate the length-specific fraction retained for sablefish. The smallest observed sablefish was 27 cm, the smallest retained sablefish was 35 cm, and an asymptote of 89.5% retained occurred at 48 cm. Less than 100%

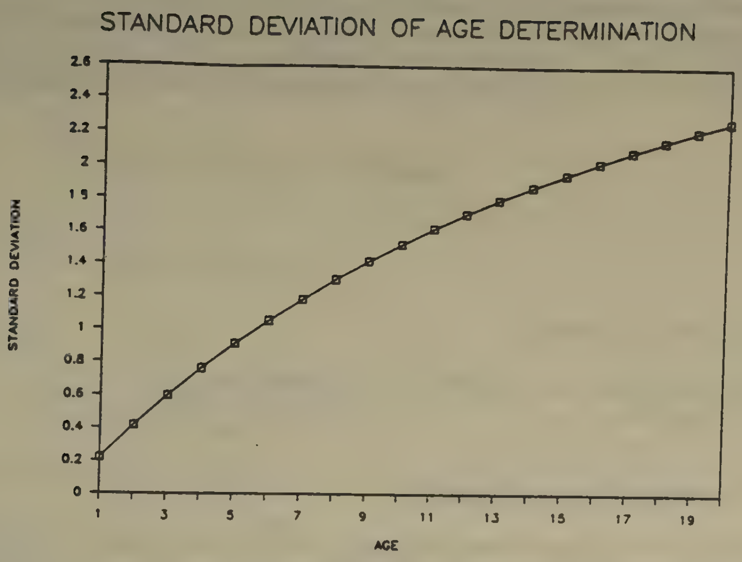


Figure 13. Ageing error calculated from reader agreement.

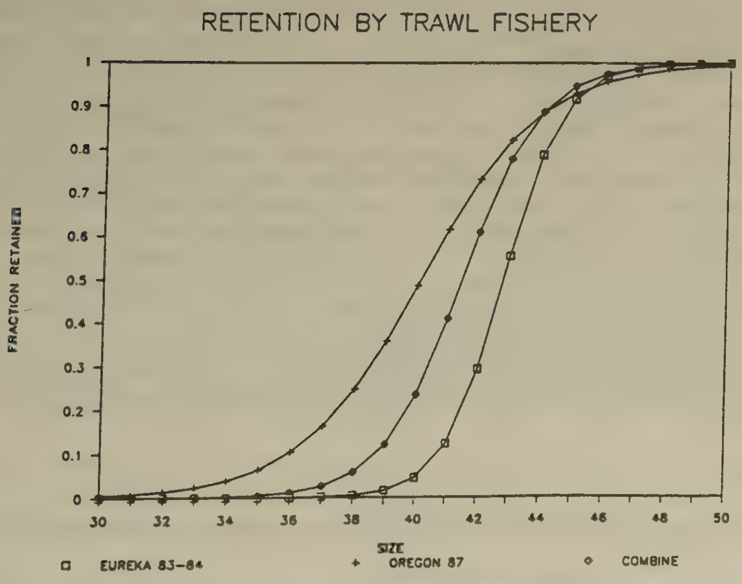


Figure 14. Retention of small fish by the trawl fishery. The 1984 data are from Fujiwara and Hankin (1984) and the 1987 data are from Pikitch (pers.comm).

retention of the larger fish is due primarily to discards which occurred after the close of the season in 1987. The values of percentage retained were divided by 0.895 to estimate the level of discard due solely to small size. A logistic function fit to these adjusted values indicates 50% retention at 40.1 cm with a slope of 0.526. Both retention functions will be investigated in the model and final model runs will utilize the average of the two functions.

Model

Subscripts

y = year
t = type of fishery or survey
a = true age
a' = category of observed age, sensitive to ageing error
l = category of length
s = sex

Vulnerability, Catchability, Availability

We note our use of the terms vulnerability, availability, selectivity, and catchability. Vulnerability means that fraction of the stock that has some positive probability of being captured. If some fish were not vulnerable, then infinite effort could not catch them. Vulnerability may be age-specific, and if vulnerability is less than 1.0 for some age, then that age fails to meet the assumption of homogeneity. Catchability is the fraction of the vulnerable stock that is captured by one unit of effort. Instead of defining catchability as being age-specific, we define catchability relative to the most available age and introduce an age-specific availability which modifies catchability for the other ages. Therefore, availability is 1.0 for at least one age and less than or equal to 1.0 for all other ages. We treat selectivity as synonomous with availability, or at least indistinguishable for it. Availability (selectivity) is an amalgam of gear avoidance, mesh retention, targeting behavior by fishermen, and geographic heterogeneity in the distribution of fishermen relative to that of each age group. For simplicity, we define that all ages are fully vulnerable to the fisheries and to the surveys, but that some ages have much lower availability (selectivity) than other ages. The consequence of this definition is that if effort was infinite, then an entire age group could be captured as long as it had non-zero availability. The distinction between vulnerability and availability is a trivial issue, however, at low levels of fishing mortality.

Model definition

The basic equations which define the dynamics of a homogeneous population follow:

Recruitment at age 1 is:

$$N_{y1} = R_y$$

where: R is recruitment
N is numbers at age

Numbers at age are:

$$N_{ya} = N_{y-1,a-1} * e^{-Z_{y-1,a-1}}$$

and for the maximum, accumulator age:

$$N_{ya} = N_{y-1,a-1} * e^{-Z_{y-1,a-1}} + N_{y-1,a} * e^{-Z_{y-1,a}}$$

where: Z is total mortality

$$Z_{ya} = M_{ya} + \Sigma_t [F_{yat}]$$

where: M is natural mortality
F is fishing mortality

Catch at age for the Tth fishery is:

$$C_{yat} = F_{yat} * N_{ya} * (1 - e^{-Z_{ya}}) / Z_{ya}$$

$$= F_{yat} * \overline{N}_{ya}$$

Catch biomass for the Tth fishery is:

$$CB_{yt} = \Sigma_a [C_{yat} * W_{yat}]$$

where: W is body weight

Numbers at age available to the Tth type of survey, conducted near the middle of the year are equal to:

$$S_{yat} = Q_t * VA_{yat} * \overline{N}_{ya}$$

where: VA is selectivity at age

Q is a scaling factor (catchability coefficient) defined as the ratio of the sum of the observed survey abundances to the sum of the estimated survey abundances.

The expected value for the Tth type of survey is:

$$SB_{yt} = Q_t * \Sigma_a [S_{yat} * W_{yat}]$$ if measured in biomass

$$SN_{yt} = Q_t * \Sigma_a [S_{yat}]$$ if measured in numbers

Here we make the following simplifications to reduce the number of parameters and to impose a well-defined pattern on the solution. Basically we assume that availability and natural mortality vary with age, but are invariant over time.

$VA_{yat} = VA_{at}$

where: $VA_{at} = 1.0$ for at least 1 age, and is ≤ 1.0 in all other ages

$M_{ya} = M_a$

$F_{yat} = E_{yt} * VA_{at}$

E is the fishing mortality rate for the most available age. E should be proportional to fishery effort by a catchability coefficient, Q.

The above equations are sufficient to describe the dynamics of a fished population. One needs only supply estimates of the vectors of recruitment, R; full fishing mortality, E; and selectivity, VA, to calculate the full time series of F, Z, C, and N. Because of the scarcity of age composition data for sablefish, we cannot directly utilize these estimates of numbers at age to determine how well the model's estimates match observations from the surveys and fisheries. We also cannot directly estimate the age-specific selectivity vectors. Instead, the model is cast primarily in terms of size composition for estimation of the selectivity vectors and for determining goodness-of-fit. Because of sex-specific differences in growth, we introduce an additional subscript, s, for sex.

Expected numbers at length in the population:

$$POPLEN_{yls} = \Sigma_a [\bar{N}_{yas} * L@A_{als}]$$

where: L@A is the distribution of length at age calculated from the growth curve and the linear increase in CV length at age

Expected numbers at length in the sample of type T:

$$SAMPLEN_{ytls} = VL_{tls} * POPLEN_{yls}$$

where: L is size-specific selectivity

Expected abundance index of type T:

$$SN_{yt} = Q_t * \{\Sigma_l \Sigma_s [SAMPLEN_{ytls}]\}$$

Note that this length-based definition replaces the age-based definition above.

Calculation of fishing mortality requires conversion of length-specific selectivity into age-specific selectivity:

$$VA_{tas} = \frac{\Sigma_l [VL_{tls} * L@A_{als}]}{\Sigma_l L@A_{als}}$$

$$= \frac{\Sigma_l [VL_{tls} * L@A_{als}]}{1.0}$$

Because of low precision in age determination, C is not the best estimate of the expected age composition for the fishery samples. Instead, C must be smeared by the estimated error in age determination:

$$\text{SAMPAGE}_{yta's} = \Sigma_a \, [C_{ytas} * \text{A'@A}_{aa's}]$$

Where A'@A is the ageing error matrix defined above.

Also, the observed weight at age for each type of survey or fishery depends on the pattern of length-specific selectivity. Especially, the fisheries tend to select only the larger individuals of the younger ages. These adjusted weights at age are needed to calculate the expected catch biomass:

$$\text{W@A}_{tas} = \frac{\Sigma_l \, [\, W_l * VL_{tls} * \text{L@A}_{als} \,]}{{}_l \, [\, VL_{tls} * \text{L@A}_{als} \,]}$$

$$= \frac{\Sigma_l \, [\, W_l * VL_{tls} * \text{L@A}_{als} \,]}{VA_{tas}}$$

Selectivity

Size-specific selectivity by each fishery and each type of survey is defined by a 3 parameter function of length:

$$VL_{tls} = \frac{(L - P1_t)}{\left\{ 1 + \left[\frac{(L-P1_t)}{(P2_t-P1_t)} \right] \wedge P3_{ts} \right\}}$$

P1 defines the length at first availability. P2 influences the rate at which selectivity increases. P3 influences the peakedness of the function. The function is scaled so that the length with maximum selectivity has a selectivity value of 1.0. Selectivity at lengths less than P1 and greater than 30 cm were given a small positive value by first calculating the selectivity at a length 5% greater than P1 then defining selectivity to increase linearly from 0.0 at 30 cm to this calculated value at 1.05 * P1.

Initially, we assumed that males and females have the same length-specific selectivity and different age-specific selectivities because of their different sizes at age. However, a better fit was consistently obtained if the males had a larger value for the P3 parameter, thus decreasing their selectivity at larger sizes and old ages. A single parameter was used to mimic this pattern:

$$P3_{ts} = P3_t + P4 * (2-s)$$

where: $s=1$ for males and $s=2$ for females.

Parameters of the selectivity function for each of the types of samples were estimated by the model.

Likelihoods

With the above equations we can calculate the goodness-of-fit between the model and the diverse data available for sablefish. We define this goodness-of-fit in terms of log likelihood, L. This puts the fit to each type of data on the same probabilistic basis so that they can more easily be combined into an overall assessment of the total goodness-of-fit.

For each type of survey abundance we assume a lognormal error, and we approximate the lognormal standard error of each survey estimate by the coefficient of variation calculated for that survey. The lognormal deviation of a given observation is:

$$DEV_{yt} = \log(OSN_{yt}/SN_{yt})$$

The log likelihood of this deviation is (ignoring a constant):

$$L_{yt} = -\,[DEV_{yt} \,/\, se_{yt}]^2 - \log[se_{yt}]$$

where: OSN is the observed survey value
se is the survey's coefficient of variation

For each survey and fishery age or length composition, we assume a multinomial error structure to define the log likelihood of that sample:

$$L_{yt} = K * \Sigma_a\, [p_{yat} * \log(p'_{yat})]$$

where: K is the minimum of 400 and the actual number of fish in the yt sample. This maximum of 400 on K follows Fournier and Archibald (1982) and Methot (1986) and prevents large samples from dominating the result.

p_{yat} is the observed proportion at age in the yt sample

p'_{yat} is the estimated proportion at age in the yt sample. It is calculated from the C_{ytas} for fishery samples and the S_{ytas} for survey samples and the ageing error matrix, A'@A, which defines the distribution of age assignments. It is the SAMPAGE from above converted to proportions.

Similarly for size compositions:

$$L_{yt} = K * \Sigma_l\, [p_{ylt} * \log(p'_{ylt})]$$

Where the p'_{ylt} are calculated from the SAMPLEN.

This multinomial error structure is also used to measure the fit to the proportion of tags returned in each year.

An extra component to the overall likelihood function is defined to force the mean of the trawl survey (small) fish to be estimated correctly. This component is calculated from the ratio of the sum of the observed abundances to the sum of the expected abundances, Q_t:

$$L_t = \frac{1.0}{1.0 + abs(log(Q_t))} - 1.0$$

Outline of model calculations

a. Recalculate the length at age matrix, L@A, for each sex if estimated growth parameters or variance have changed.
b. Recalculate the ageing error matrix, A'@A, if estimated ageing error parameters have changed.
c. Recalculate the length-specific selectivities, VL, if any of the pertinent parameters have changed.

i. then recalculate the equivalent age-specific selectivities, VA, as the mean of the VL weighted by the distribution of length at age, L@A.

ii. recalculate the expected mean body weight at age for each sample type, W@A, from the population length at age distribution, L@A, the body weight at length equation, and the length specific selectivities, VL.

d. Use the current estimate of natural mortality and virgin recruitment to calculate the virgin age composition and virgin spawning biomass for use in the stock-recruitment relationship. Then assume knife-edge recruitment to the fishery and iteratively calculate the fishing mortality which produces an equilibrium yield of 3512 mt. This equilibrium state is the starting point in 1970.

For each subsequent year

Note that all of below occurs for each sex.

a. Graduate the survivors from last year into the next age category; except accumulate in the age 20+ category.

b. Get the age 1 yearclass abundance in one of two ways:

i. Use the stock-recruitment relationship and last year's spawning biomass.

ii. Use the mean recruitment level multiplied by a recruitment factor for that year. These recruitment factors are parameters to be estimated by the model. Recruitment factors are used only for years which are followed by an adequate amount of age and length data. We will estimate recruitments for the 1977 through 1985 yearclasses. Earlier and later yearclasses will be calculated from the stock-recruitment relationship.

c. Assume that age-specific fishing mortality by each type of fishery is the product of a type,age,sex-specific selectivity, VA(tas), and effort, E(yt). Calculate age,sex-specific total mortality, Z(as), as the sum of natural mortality and each of the type, age, sex-specific fishing mortalities.

d. For each age and sex, calculate the mean population numbers and surviving numbers.

e. For each type of fishery, use the mean population numbers, weight at age for that type, fishing mortality, and fraction retained by the trawl fishery to calculate the total retained catch biomass and the total discarded biomass.

f. For each type of fishery, compare the estimated total catch biomass to the observed total catch biomass. If the ratio differs from 1.0, then use the ratio to adjust the estimated effort for that type of fishery and redo above steps c-e until the observed and estimated catch biomasses are within 0.1% of each other.

g. If there was a pot survey or tri-ennial survey in that year, then use the mean numbers at length and the length-specific selectivities to calculate the sample catch you would expect from a survey of that type. These estimated abundances will be adjusted by the recalculated Q before comparison to the observed survey values.

h. If there was an age composition observation in that year, then use the mean numbers at age and the age-specific selectivities for that type of observation to calculate an expected sampled age composition. Then use the A'@A key to convert this expected sampled age composition to an expected observed age composition. Pool for ages 10+ because of the low precision in the age determinations and because recruitments prior to 1977 are not individually estimated. Calculate the log likelihood of the observed age composition and sum with log likelihoods for this type of data in other years.

i. If there was a length composition observation in that year, then use the length at age key to convert the mean numbers at age in the population to the length composition of the population. Then use the type, length-specific selectivities to calculate an expection for the sampled, observed length composition. Calculate the log likelihood of the observed length composition and sum with log likelihoods for this type of data in other years.

j. Calculate the total fishing mortality for ages 5+, weighted by the abundance at each age and sex. This mortality will be used to calculate the expected number of tags returned in this year.

k. Calculate spawning biomass of females from the numbers at age at the beginning of the year (when spawning occurs), weight at age, and fraction mature.

l. Goto step 2.a. for the next year.

3. For each type of survey, recalculate Q before calculating the deviations between the individual observed and estimated survey abundances. Q is fixed at 1.0 for the survey that is defined as fully quantitative, the abundance of 32-41cm sablefish in the tri-ennial trawl surveys.

4. For each year in which tags were released, calculate the expected percentage returned in each subsequent year from the time series of age 5+ mortalities. The following FORTRAN statements accomplish this task:

```
      TAGSOUT=1.0
      RELRET=0.0
      LIKE(Y,T)=0.0

      DO 800 Y1 = Y+1,LYR
        Z = F5(Y1) + NATMORT + TAGLOSS
        ERETURN(Y1) = TAGSOUT * F5(Y1)/Z * (1.0-EXP(-Z))
        RELRET = RELRET + ERETURN(Y1)
800     TAGSOUT = TAGSOUT * EXP(-Z)
        DO 810 Y1 = Y+1,LYR
          ERETURN(Y1) = ERETURN(Y1)/RELRET
810       LIKE(Y,T) = LIKE(Y,T)+ORETURN(Y,Y1)*ALOG(ERETURN(Y1))
```

where Y is the release year, LYR is the last year for which there are returns from this release, ORETURN is the observed number of returns in year Y1 from release year Y, F5 is the fishing mortality for ages 5+ combining both gear types and weighting F at age by the abundance at that age, ERETURN/RELRET is the expected percentage of these returns that should occur in year Y1. TAGSOUT is proportional to the effective initial number of tags and its value does not matter.

5. Calculate the likelihood component for the mean trawl survey (small) from the Q for this type of survey.

6. Calculate the likelihood for the stock-recruitment relationship from the log(estimated/expected) for 1977 - 1985, the years with individual recruitment estimates. Use a standard error value of 0.40 for calculation of the log likelihood.

Total log likelihood

The log likelihoods for each type of data are multiplied by their assigned emphasis factor then summed to provide the current value for the overall log-likelihood. The emphasis factors for each component were set equal to 1.0 with the following exceptions. Goodness-of-fit to a stock-recruitment relationship was calculated, but assigned an emphasis of 0.001 so that it would not affect the parameter estimates. The importance of the trawl survey (small) is solely to set the mean level of recruitment for the survey years. Therefore, the likelihood of the deviations in individual years is given a nil emphasis of 0.001, and the fit to the size composition which contributes to this subset of the trawl survey is not even calculated. Instead, the emphasis on the fit to the mean of the trawl survey (small) is started at a high (100) value, then reduced within the run as the fit to the mean stays at a good level (>-0.02). Although the age and length compositions each have an emphasis of 1.0, they have already been deemphasized by scaling each individual sample so that the total number of fish measured (or aged) is a maximum of 400 in each sample. Note that the total number of fish measured (aged) acts as a multiplier on the log likelihood for that sample. Because the multinomial error model ignores process error, it is unreasonable to allow a sample with a large sample size to be given extremely high emphasis.

Parameter Estimation

The parameters which maximize the above overall log likelihood are found by an iterative procedure that utilizes numerical estimates of the first derivatives and Hessian matrix of mixed partial derivatives. In this adaptation of the Gauss-Newton procedure, the amount by which to change the parameters is calculated by inverting the Hessian matrix and post-multiplying by the first derivatives. The procedure works well and generally converges in fewer iterations than the number of parameters (26). However, this numerical, brute-force approach is time-consuming. On a 20 Mhz micro-computer with math co-processor, evaluation of the likelihood function takes about 1 second. But a very large number of evaluations are necessary to calculate all the derivatives so, even with numerous short-cuts, the total run time is 15 min to 1 hour.

Results

The configuration of the model included the parameters and coefficients listed in Tables 6 and 7. Evaluation of the model's ability to match the sablefish database proceeded in several stages. Most of these stages occurred in the preliminary scenario, then a small subset were evaluated in the final scenario. The differences between the two scenarios are as follows: (1) extra juvenile mortality - none in the preliminary scenario, estimated in the final scenario; (2) area expansion of the trawl survey - none in the preliminary and 6.5% expansion to Pt. Conception in the final runs; (3) size at age 5 - revised downwards in final runs due to bias detected in preliminary runs and because the L_5 used in the preliminary runs was based on the growth curves fit to the 1983 and 1985 pot survey data rather than the observed mean size at age 5 in these two surveys; (4) maximum size - best values were estimated in the first stage of the final scenario to be less than the values used in the preliminary scenario. The expected impact of the differences between the two scenarios is that juvenile mortality will decrease estimated population biomass, area expansion will increase biomass, and decreased growth and decreased maximum size will decrease biomass.

Preliminary scenario

Incomplete models

The first set of runs in the preliminary scenario was designed to gradually relax the assumptions made in past analyses. The first run was designed to mimic stock reduction analysis, albeit in a cumbersome age-structured manner (Table 8). All recruitments were taken from the stock-recruitment relationship, only the fit to the mean abundance in the 3 tri-ennial surveys was considered, the fixed gear selectivity was set nearly at knife-edge at age 3, trawl selectivity was set so that the peak occurred at 44-45 cm and gradually declined for larger fish, and the only parameter estimated was the level of virgin recruitment. Hence we are calculating the virgin recruitment level that would produce the mean of the 3 observed recruitments and be consistent with the observed time series of fishery removals. The resultant estimate of age 3+ biomass in 1988 is 127,000 mt, down from 240,000 mt in 1970. The fit of this simple model to the individual surveys and to the age and length compositions is poor. When the survey selectivities and, especially, the fishery selectivities are estimated, there are large improvements to the fit to these data but little change in the estimated abundance. Fitting the individual recruitments during 1977 - 1985 results in a smaller improvement to the overall likelihood function and a decrease in the level of abundance. The improved fit obtained by estimating individual recruitments is due to the model's ability to match the scant information on variation in year class strength. Because the improvement is small, it seems that either variation in recruitment has not been great or that the various types of data are not consistent in indicating which years had good recruitments. When individual recruitments are estimated, the model is now able to estimate that the mean recruitment during the period 1977 - 1985 was less than the mean of the recruitments observed in 1980, 1983, and 1986. This causes mean biomass to be lower and to decline more rapidly, thus improving the fit to the declining pot index.

Table 6. Constants in the sablefish synthesis model.

	Preliminary	Final
Male growth:		
Length at age 1	38.4	38.4
Length at age 5	52.3	52.0
Asymptotic length	70.0	64.5
c.v. length at age 1	0.068	0.068
c.v. length at age 20	0.0902	0.0902
Female growth:		
Length at age 1	38.4	38.4
Length at age 5	57.3	56.2
Asymptotic length	85.0	77.5
c.v. length at age 1	0.068	0.068
c.v. length at age 20	0.1452	0.1452
Length-Weight power function		
intercept	2.3319E-6	2.3319E-6
slope	3.3639	3.3639
Maturity-Length logistic function		
slope	0.2491	0.2491
Length at 50% maturity	58.3	58.3
Trawl fishery logistic retention function		
slope	0.809	0.809
Length at 50% retention	41.4	41.4
Asymptotic retention	1.00	1.00
Trawl survey are multiplier	1.000	1.065
Long-term tag loss rate	0.100	0.100
Stock-recruitment density dependence	0.889	0.889
Ageing error saturation function		
parameter 1	0.223	0.223
parameter 2	4.345	4.345
Catch multiplier	1.000	1.000

Table 7. Parameters estimated by numerical calculation of derivatives to the overall log likelihood, except natural mortality, trawl fishery P1, and trawl survey P1 were fixed at the indicated values and were not changed within a run and recruitment multipliers expressed as negative values are simply calculated from the spawner-recruitment curve and are not individually estimated. Recruitments are expressed as multiples of the mean recruitment.

		Initial value	Final value
Nat mort		0.15	0.15
Juve mort		0.04	0.012
Male effect		1.50	1.717
Fixed	P1	45.0	44.4
	P2	65.0	67.2
	P3	4.0	2.154
Trawl	P1	36.0	36.0
	P2	50.0	57.6
	P3	4.0	4.215
Trawl Surv	P1	24.0	24.0
	P2	38.0	38.3
	P3	3.0	3.354
N pot	P1	45.0	43.8
	P2	55.0	54.2
	P3	2.5	2.144
S pot	P1	45.0	42.9
	P2	55.0	53.4
	P3	2.5	2.499
Virgin Recr.		9500.	9522.
Mean Recr.		9500.	9560.
Recr 69		-1.0	-0.971
Recr 70		-1.0	-0.971
Recr 71		-1.0	-0.971
Recr 72		-1.0	-0.971
Recr 73		-1.0	-0.968
Recr 74		-1.0	-0.966
Recr 75		-1.0	-0.962
Recr 76		-1.0	-0.955
Recr 77		1.5	1.598
Recr 78		0.5	0.217
Recr 79		1.5	1.763
Recr 80		1.5	1.345
Recr 81		1.0	0.819
Recr 82		1.0	0.838
Recr 83		0.5	0.650
Recr 84		0.5	0.499
Recr 85		1.5	1.266
Recr 86		-1.0	-0.841
Recr 87		-1.0	-0.827

Table 8. Summary of synthesis model runs. The values displayed are estimated virgin recruitment, estimated mean recruitment for the 1977 - 1985 year classes, biomass for ages 3+ in 1970 and 1988 (values are mean within year, not beginning of year), fishing mortality for ages 5+ which is used to calculate expected tag returns, the overall log likelihood calculated using the standard emphasis factors, and for the northern pot index the log likelihood of the time series and the expected survey value for 1987.

Title	Recruitment		Age 3+ Biomass		Age 5+ F in 1988	Total Like	Northern Pot	
	Virgin	Mean	1970	1988			Like	E(87)
Incomplete models								
SRA MIMIC	10969	N/A	240	127	0.073	-3293	-34	6.3
FIT SURVEY	11470	N/A	253	120	0.065	-2672	-33	6.0
FIT SURVEY & FISH	10817	N/A	236	124	0.085	-1341	-35	6.6
FIT SURVEY & RECR	7136	10234	141	54	0.149	-2601	-18	5.8
Preliminary "best" model								
NULL START	8987	9080	189	86	0.122	-1196	-21	5.6
GOOD START (LOW VR)	9688	9286	207	95	0.111	-1196	-20	5.4
GOOD START (HIGH VR)	9825	9284	210	95	0.111	-1195	-19	5.3
No forcing on mean trawl survey small fish								
GOOD START	8913	7955	187	68	0.155	-1192	-18	4.8
GOOD START (LOW VR)	8463	7253	175	54	0.192	-1192	-17	4.4
GOOD START (HIGH VR)	9478	8752	201	84	0.126	-1192	-19	5.2

Table 8 continued.

	Recruitment		Age 3+ Biomass		Age 5+ F in	Total	Northern Pot	
Title	Virgin	Mean	1970	1988	1988	Like	Like	E(87)
Emphasis runs								
STOCK-RECR 10x	9887	9370	212	101	0.104	-1212	-23	5.8
STOCK-RECR 0.1X	9493	9185	202	92	0.114	-1199	-19	5.5
TAG RETURN 100x	12429	11348	277	141	0.077	-2064	-40	6.5
TAG RETURN 10x	9497	9168	202	94	0.111	-1206	-23	5.8
TAG RETURN 0.1x	9864	9298	211	95	0.111	-1195	-19	5.3
TRL SURV 10x ALL	10774	10320	235	111	0.096	-1255	-15	4.7
TRL SURV 0.1x ALL	9330	8702	198	85	0.123	-1207	-20	5.5
TRL SURV 10x ABUND	9893	9216	212	94	0.112	-1195	-19	5.2
TRL SURV 0.1x ABUND	9604	9195	205	92	0.114	-1193	-20	5.4
POT SURV 10X ALL	5924	7699	109	49	0.227	-1441	-27	6.4
POT SURV 0.1X ALL	19796	12447	466	235	0.046	-1394	-23	3.7
POT SURV 0.1X ABUND	9482	9248	201	93	0.113	-1194	-21	5.6
POT SURV 5X ABUND	9630	8577	205	80	0.118	-1213	-12	4.6
POT SURV 10X ABUND	8841	7757	185	58	0.174	-1265	-6	4.1
POT SURV 25X ABUND	8817	7610	184	52	0.189	-1390	3	3.7
FISHERY 10X	22205	13315	528	272	0.040	-1452	-28	3.6
FISHERY 0.1X	6408	8027	121	57	0.186	-1318	-26	6.4
AGE COMP 10X	8957	8174	188	89	0.116	-1603	-27	6.0
AGE COMP 0.1X	7754	8986	157	67	0.157	-1338	-22	5.9
LEN COMP 10X	7480	9408	149	71	0.150	-1386	-27	6.5
LEN COMP 0.1X	9592	8056	204	91	0.113	-1579	-19	5.3

	Recruitment		Age 3+ Biomass		Age 5+ F in	Total	Northern Pot	
Title	Virgin	Mean	1970	1988	1988	Like	Like	E(87)
Sensitivity to biological and other constants								
BIOLOGY - SET-UP	9528	9122	202	91	0.116	-1193	-20	5.4
LARGE MALES 75	9404	8953	205	91	0.118	-1228	-20	5.4
SMALL MALES 65	9606	9228	198	91	0.116	-1176	-20	5.5
FAST MALES L5=54.3	10232	9592	231	110	0.092	-1275	-19	5.3
SLOW MALES L5=50.3	9021	8619	180	72	0.148	-1159	-21	5.3
LARGE FEMALE 90	9451	9117	209	94	0.114	-1218	-20	5.4
SMALL FEMALE 80	9531	9068	194	85	0.120	-1177	-20	5.4
FAST FEMALE L5=59.3	9695	9484	221	108	0.098	-1240	-20	5.6
SLOW FEMALE L5=55.3	9232	8556	180	71	0.147	-1181	-20	5.1
NATURAL MORT=.175	11068	9204	180	66	0.155	-1222	-19	4.7
NATURAL MORT=.125	7678	8734	219	113	0.096	-1177	-22	6.1
NATURAL MORT=.100	6419	8604	263	155	0.073	-1177	-25	6.7
EXTRA JUVEMORT=.05	9902	9302	193	79	0.132	-1195	-19	5.1
EXTRA JUVEMORT=.15	11401	10393	189	74	0.141	-1199	-19	5.0
LOWER AGE ERROR	10121	9347	218	101	0.104	-1209	-23	5.5
HIGHER AGE ERROR	9472	8932	201	87	0.120	-1190	-21	5.3
CATCH MULT = 1.05	9708	9247	207	88	0.126	-1193	-19	5.3
CATCH MULT = 1.20	10279	9400	221	77	0.163	-1189	-18	4.8
MAX TWL RETAIN=.95	9559	9162	203	88	0.123	-1193	-19	5.3
MAX TWL RETAIN=.90	9618	9220	205	85	0.130	-1192	-19	5.2
TAGLOSS=.15 (10x)	11730	9731	259	123	0.109	-1222	-22	5.4
TAGLOSS=.05 (10x)	8077	8687	165	77	0.173	-1211	-25	6.2
TWL RECR SIZE=38	9394	8875	199	87	0.121	-1203	-20	5.3
TWL RECR SIZE=34	9549	9280	203	91	0.115	-1194	-19	5.4
TRL RECR SIZE=26	9548	9176	203	91	0.115	-1194	-20	5.4
TRL RECR SIZE=22	9512	9134	202	91	0.116	-1194	-20	5.4

Table 8 continued.

	Recruitment		Age 3+ Biomass		Age 5+ F in	Total	Northern Pot	
Title	Virgin	Mean	1970	1988	1988	Like	Like	E(87)
FOLLOWING RUNS USE NO FORCING ON THE MEAN TRI-SMALL								
START 9300 7000	9402	9083	199	90	0.116	-1198	-20	5.5
START 8000 7000	9302	8255	197	76	0.137	-1193	-18	4.9
START 10000 7000	9358	8982	198	88	0.119	-1198	-20	5.4
START 11000 9000	9485	9365	201	95	0.110	-1215	-21	5.7
START 8000 6000	9000	8227	189	73	0.140	-1192	-18	5.0
STOCK-RECR 10x	9771	9234	209	99	0.107	-1216	-23	5.8
STOCK-RECR 0.1X	9618	9158	205	94	0.113	-1196	-20	5.5
TAG RETURN 10x	9359	8570	198	86	0.121	-1210	-22	5.6
TAG RETURN 0.1x	9486	8986	201	89	0.118	-1198	-20	5.3
TRI SURV 10x ALL	9460	8060	201	65	0.162	-1270	-14	3.7
TRI SURV 0.1x ALL	9642	9157	205	96	0.109	-1211	-21	5.7
TRI SURV 10x AB	9293	8562	196	81	0.129	-1199	-18	5.1
TRI SURV 0.1x AB	9084	8741	191	82	0.127	-1198	-20	5.4
POT SURV 10x ALL	5906	6108	108	25	0.431	-1446	3	4.5
POT SURV 0.1X ALL	18158	14117	424	241	0.045	-1378	-22	4.2
POT SURV 25x AB	7918	6595	161	33	0.289	-1386	1	3.3
POT SURV 10x AB	8198	6789	168	40	0.247	-1260	-6	3.6
POT SURV 5x AB	8397	7116	173	49	0.208	-1217	-11	4.0
POT SURV 0.1X AB	10009	10706	215	121	0.087	-1200	-25	6.3
FISHERY 10x	43783	31344	1079	765	0.015	-1417	-26	4.6
FISHERY 0.1x	6170	6345	116	31	0.334	-1333	-19	4.7
AGE COMP 10x	12140	16493	270	244	0.043	-1607	-39	8.4
AGE COMP 0.1x	7455	7455	149	42	0.245	-1346	-16	4.7
LEN COMP 10x	6507	7887	124	43	0.241	-1444	-23	5.7
LEN COMP 0.1x	9259	8170	196	91	0.111	-1596	-21	5.6

Table 8 continued.

	Recruitment		Age 3+ Biomass		Age 5+ F in	Total	Northern Pot	
Title	Virgin	Mean	1970	1988	1988	Like	Like	E(87)
FOLLOWING RUNS DELETE ONE SURVEY OR FISHERY SAMPLE								
NULL, NO DELETIONS	9596	8893	204	87	0.121	-1195	-19	5.2
DEL 71 N POT SURV	12512	9567	279	127	0.085	-1089	-20	5.0
DEL 79 N POT SURV	9844	9867	211	102	0.104	-1095	-21	4.9
DEL 80 TRAWL SURV	9651	8825	206	89	0.117	-1112	-18	5.4
DEL 80 N POT SURV	9856	9586	211	100	0.106	-1187	-20	5.6
DEL 81 N POT SURV	9632	8785	205	88	0.120	-1145	-13	5.7
DEL 83 TRAWL SURV	9400	9002	199	89	0.118	-1149	-21	5.5
DEL 83 N POT SURV	10722	9916	233	116	0.092	-1097	-9	5.3
DEL 84 S POT SURV	9486	9301	201	96	0.110	-1170	-22	5.7
DEL 85 N POT SURV	11224	10337	246	120	0.089	-960	-18	4.8
DEL 86 FIXED FISH	9081	8931	191	90	0.115	-1146	-21	5.7
DEL 86 TRAWL FISH	8620	8975	179	83	0.126	-1120	-21	5.8
DEL 86 TRAWL SURV	9437	9654	200	101	0.104	-1119	-23	6.1
DEL 86 S POT SURV	9541	9350	203	96	0.109	-1154	-22	5.7
DEL 87 FIXED FISH	8438	9122	174	83	0.127	-1046	-24	6.1
DEL 87 TRAWL FISH	8250	9099	176	83	0.126	-1048	-22	6.1
DEL 87 N POT SURV	9307	9511	197	95	0.110	-1172	-7	6.1

Table 8. continued.

The following set of final runs have these characteristics:

1. increase survey abundances by 6.5% for the Conception expansion
2. include extra natural mortality on juveniles
3. change L5 values to 52.0 for males, 56.4 for females

Title	Recruitment		Age 3+ Biomass		Age 5+	Total	Northern Pot	
	Virgin	Mean	1970	1988	F in 1988	Like	Like	E(87)
Find best L values								
M 65 F 76	9910	9710	176	76	0.132	-1142	-20.4	5.36
M 65 F 78	10133	9789	179	80	0.127	-1141	-20.5	5.42
M 65 F 80	9853	9671	177	74	0.136	-1145	-19.7	5.32
M 65 F 82	9977	9695	180	79	0.13	-1151	-20.3	5.42
M 62 F 79	10223	9735	177	79	0.128	-1153	-20.4	5.43
M 64 F 79	9922	9751	176	76	0.133	-1141	-20.7	5.4
M 66 F 79	10113	9521	178	77	0.132	-1146	-20.2	5.35
M 68 F 79	9651	9609	177	74	0.137	-1156	-20.2	5.36
Select best L as M 64.5, F 77.5								
Final Runs. THE FIRST OF THESE IS SELECTED AS THE BEST FINAL RUN								
virg-recr=8000	9522	9560	176	79	0.126	-1143	-20.2	5.54
virg-recr=11000	10249	9913	175	79	0.128	-1153	-20.7	5.5
pot abund 10x	9716	8369	163	48	0.199	-1224	-7.3	4.03
age comp 0.1x	8947	9998	145	65	0.156	-1247	-22.7	5.84
natmort = .17	11861	10143	176	68	0.144	-1170	-19	4.87
natmort = .13	8426	9436	175	85	0.119	-1128	-22.3	5.97
natmort = .11	7267	9405	175	91	0.114	-1095	-23.9	6.44

Preliminary best model

The model is able to converge on approximately the same "best" point from a range of starting points (Table 8): initial selectivities are knife-edge and initial recruitments are from stock-recruitment relationship (null start), good starting values but a low initial guess for virgin recruitment (good low start), or good starting values and a high initial guess for virgin recruitment (good high start). The end result is sensitive to the starting virgin recruitment level when run without the extra likelihood component which forces a near perfect fit to the mean of the trawl survey (small). Without this forcing, the estimated recruitment levels are lower which causes a more rapid decline in biomass and a better fit to the pot index surveys. Note that the overall likelihood is the same for these three different levels of virgin recruitment. The patterns of estimated selectivity in this model largely match our prior expectations (Table 9): smaller fish are more available to the trawl fishery than to the fixed gear fishery, maximum availability to the trawl survey (all) occurs for the size range of the age 1 fish then trails off rapidly throughout the size range of the age 2 and 3 fish, the size range of the age 1 and age 2 fish is barely available to the pot index, peak availability to the pot index occurs for the size range of ages 4-6, availability to the southern pot index is displaced slightly towards smaller fish relative to the northern pot index.

Varying Emphasis

The level of emphasis placed on each type of data can influence the nature of the final solution if the various types of data are not completely consistent with each other. If all of the components of the overall log likelihood function are correctly specified, then placing equal emphasis on each type should achieve the best compromise solution among the various types of data. However, we have already noted that the multinomial model used to specify the error structure for the age and length compositions will tend to overestimate confidence in these samples. Certainly other simplifications in the model will distort the correctness of the likelihood definitions. Here we will explore the sensitivity of the overall result to variation in the emphasis placed on each type of data. In each of the following runs the emphasis on some likelihood component is changed. To facilitate comparison of results, we also calculate the overall likelihood with the original, standard emphasis factors. These likelihoods are presented in Table 8.

1. Stock-recruitment. The basic model largely ignored the fit to this function, the emphasis was only 0.001. Raising the emphasis to 1.0 degraded the overall likelihood by only about 5 units. Raising the emphasis to 10.0 tended to reduce the variation in the estimated recruitments as they were pulled closer to the stock-recruitment relationship. This degraded the fit and raised the ending biomass, similar to the above models in which the all recruitments were taken directly from the stock-recruitment relationship.

2. Tag return. Reducing this emphasis to 0.1 had no effect on the model. Increasing the emphasis to 10.0 slightly degraded the fit but did not substantially change the estimated stock abundance. However, increasing the emphasis to 100.0 caused a large increase in estimated abundance and a great degradation in the overall likelihood.

Table 9. Size specific selectivities in preliminary model. The trawl survey (small) selectivities are fixed at the indicated values and are not estimated. The trawl fishery retention fractions are calculated from a logistic function and are not estimated in the model.

Length	Fishery		Trawl Survey		N. Pot	S. Pot	Trawl
	Fixed	Trawl	small	all			retain
	Male Selectivities						
32.0- 36.0	.003	.005	1.000	.971	.005	.005	.007
36.0- 38.0	.005	.073	1.000	1.000	.009	.009	.036
38.0- 40.0	.006	.209	1.000	.852	.012	.011	.152
40.0- 42.0	.007	.349	1.000	.661	.014	.013	.431
42.0- 44.0	.009	.488	.000	.484	.017	.078	.755
44.0- 46.0	.066	.626	.000	.347	.143	.302	.934
46.0- 48.0	.220	.758	.000	.248	.456	.616	.986
48.0- 50.0	.414	.877	.000	.179	.796	.878	.997
50.0- 52.0	.602	.965	.000	.131	1.000	1.000	.999
52.0- 54.0	.774	1.000	.000	.097	.986	.926	1.000
54.0- 56.0	.910	.964	.000	.073	.807	.723	1.000
56.0- 58.0	.989	.859	.000	.056	.591	.509	1.000
58.0- 60.0	1.000	.710	.000	.044	.416	.345	1.000
60.0- 64.0	.888	.491	.000	.031	.259	.206	1.000
64.0- 68.0	.670	.271	.000	.020	.138	.103	1.000
68.0- 72.0	.462	.146	.000	.014	.080	.056	1.000
72.0- 76.0	.312	.081	.000	.010	.050	.033	1.000
76.0- 80.0	.214	.047	.000	.007	.033	.021	1.000
80.0- 90.0	.128	.023	.000	.004	.020	.012	1.000
90.0-100.0	.080	.011	.000	.003	.012	.007	1.000
	Female Selectivities						
32.0- 36.0	.003	.005	1.000	.963	.006	.005	.007
36.0- 38.0	.005	.079	1.000	1.000	.010	.010	.036
38.0- 40.0	.007	.227	1.000	.924	.013	.012	.152
40.0- 42.0	.008	.378	1.000	.818	.016	.015	.431
42.0- 44.0	.010	.527	.000	.705	.019	.087	.755
44.0- 46.0	.074	.671	.000	.599	.155	.333	.934
46.0- 48.0	.246	.802	.000	.506	.474	.657	.986
48.0- 50.0	.454	.909	.000	.427	.782	.893	.997
50.0- 52.0	.640	.979	.000	.362	.955	1.000	.999
52.0- 54.0	.792	1.000	.000	.308	1.000	.987	1.000
54.0- 56.0	.903	.970	.000	.264	.962	.898	1.000
56.0- 58.0	.971	.897	.000	.228	.884	.782	1.000
58.0- 60.0	1.000	.796	.000	.198	.795	.667	1.000
60.0- 64.0	.981	.633	.000	.163	.672	.526	1.000
64.0- 68.0	.908	.442	.000	.127	.536	.383	1.000
68.0- 72.0	.808	.302	.000	.101	.435	.286	1.000
72.0- 76.0	.708	.208	.000	.082	.359	.220	1.000
76.0- 80.0	.617	.146	.000	.067	.303	.174	1.000
80.0- 90.0	.497	.090	.000	.050	.237	.126	1.000
90.0-100.0	.418	.057	.000	.040	.197	.097	1.000

3. Tri-ennial trawl survey. Tenfold increase or decrease in the emphasis on just the abundance estimates had no effect on the model. Apparently these observations are highly consistent with other data in the model. Increasing or decreasing the emphasis on survey abundance and length composition by tenfold caused a degradation in the overall likelihood, but a different effect on estimated abundance. High emphasis on all trawl survey data caused higher estimated abundance and, unexpectedly, an improved fit to the pot index abundance.

4. Pot surveys. Increasing the emphasis on all pot survey abundance, length composition and age composition data produced a poor overall fit and an unreasonable result with a very low level of virgin recruitment. This may be due to an improved fit to the 1971 northern pot index size composition because, note below, that deletion of the 1971 northern pot index data caused a high estimate of virgin recruitment. Conversely, reducing the emphasis on all pot index data also produced a poor overall fit, but with a very high level of estimated abundance. A very consistent, monotonic result occurred when the change in emphasis was only on the abundance aspect of the pot index survey. Higher emphasis on the abundance in the pot index caused a much improved fit to this type of data, a degraded overall fit, and a decrease in the estimate of current biomass.

5. All fishery data. The overall result was highly sensitive to the emphasis placed on the fishery age and size composition data. Primarily because the great abundance of older fish in the fisheries is at odds with the declining pot index and the lack of older fish in the 1983 and 1985 pot index surveys. Note that the break-and-burn technology for reading sablefish otoliths is still evolving. A change in ageing criteria occurred between the time the 1986 port samples were read and the 1987 port samples were read. The magnitude of the change is not known and it is likely that only older fish are affected. Some otoliths previously read by the old criteria are being re-read so that a calibration can be developed.

6. All age composition or all size composition data. The estimated biomass was not overly sensitive to the emphasis placed on all the age composition data or on all the size composition data. But the overall fit to the model is substantially degraded if the emphasis on all age composition or all size composition is changed. We see no reason for setting these emphasis factors at anything other than 1.0.

Model Sensitivity to Constants

In the next stage of the preliminary runs we investigated the model's sensitivity to various fixed coefficients.

1. Growth. Faster and slower growth and maximum size was investigated for each sex (Table 8). Better fits and substantially lower biomasses were obtained at slower growth or smaller maximum size for each sex. On the basis of this result we reexamined the information available on size at age 5 and made small adjustments for the final scenario and we decided to use the model to determine which values for maximum size gave the best fit.

2. Natural mortality. A better fit and substantially higher biomass was obtained at lower levels of natural mortality. Most of the improved fit was due to a better match to the high frequency of old fish in the 1987 fishery samples. The fit to the pot index surveys was degraded at lower levels of natural mortality because with more old fish in the population the estimated pot index cannot change nearly as rapidly as the observations changed. At low levels of natural mortality an unexpected result occurs. Estimated virgin recruitment is substantially less than the estimated mean level of recruitment during 1977-1985. This occurs because virgin recruitment and natural mortality determine the relative abundance of older fish at the end of the time series, when most of the data wre collected. With lower M, virgin recruitment also must be lower otherwise there will be too many old fish in the population. Although a better overall fit is obtained at lower levels of natural mortality, the poor fit to the pot index and the low estimate for virgin recruitment suggest that the natural mortality equal to 0.15 is more realistic for the WOC portion of the sablefish population.

Introducing additional natural mortality on juveniles had an insignificant effect on the fit and lowered the estimated current biomass. The major impact was on the estimated level of recruitment. This occurs because the recruitment values are referenced to the beginning of the year, but the recruitment measurements (i.e. the trawl survey (small)) are referenced to the mean abundance within the year. The extra natural mortality on juveniles has a large impact on the ratio of initial numbers to mean numbers so at higher levels of juvenile mortality the estimated initial numbers must be increased to maintain a good match with the observed mean numbers.

3. Ageing error. Changing the level of ageing error had only a small effect on estimated biomasses or the goodness of fit.

4. Catch multiplier. Increasing all of the catch biomasses (trawl and fixed) by 5 or 20% had the expected effect of decreasing the estimated current biomass because mean recruitment is fixed by the 3 observed recruitments. This decrease in recent levels of biomass improves the fit to the pot index and, slightly, to the overall likelihood. If there is evidence that historical landings were underreported by more than 5%, then this factor should be incorporated in the analysis.

5. Trawl discard. In 1987 there is evidence that about 10.5% of large sablefish were discarded by the trawl fishery, presumably most of this occurred at the end of the year after the sablefish quota had been reached. If we assume that similar levels of discard occurred historically, then the model estimates a small reduction in the current biomass. In next year's version of the sablefish model we should make provisions for yearly changes in the amount of sablefish discarded after the close of the season.

6. Tag loss. Increasing or decreasing the long term level of tag loss causes a degradation in the overall likelihood. Note that these runs used a 10x emphasis on the tag return data, so the default for comparison is the emphasis run called TAG RETURN 10x. Estimated biomass is positively correlated with the level of tag loss for the following reason: if tag loss is lower than the default value of 0.1 then, in order for the model to maintain a good match to the observed pattern of tag returns, it must decrease estimated biomass thus

increasing estimated fishing mortality thus increasing the rate at which tags are removed from the tagged population.

7. First availability. The model has difficulty in estimating the size at which sablefish first become available to the trawl fishery. This occurs because the retention goes to zero for the small fish so one cannot tell the difference between not catching any small fish and catching and discarding many small fish. In fact, the model prefers the latter scenario because it allows it to kill off many small fish, driving the biomass down and achieving a better fit to the declining pot index. We found it necessary to fix the size at first availability at a reasonable value (36 cm). Table 8 indicates that any value in the range 34 - 38 cm would have the same result. The model also had difficulty with estimating the size at first availability to the tri-ennial trawl survey probably because the model ignored fish less than 32 cm and the first category, 32-35 cm, was 4 cm wide. We found that values in the range 22-26 cm gave the best shape to the availability function for larger sizes and all runs were done with this availability parameter set at 24 cm.

Model Sensitivity to Data

The influence of individual surveys and fishery samples was investigated by deleting one survey or fishery sample then running the model without that observation. Note that in Table 8 the reported likelihoods cannot be readily compared because the likelihoods are total likelihoods and are not likelihoods per observation. When a deletion was made, all types of data (abundance, size composition, and age composition) were deleted at the same time. Among these 16 runs, the mean age 3+ biomass in 1988 was 97,000 mt (s = 13,000). The minimum was 83,000 mt which occurred when the 86 trawl fishery samples, or the 87 trawl fishery, or the 87 fixed gear fishery samples were deleted. The maximum was 127,000 mt which occurred with deletion of the 1971 northern pot survey, and large biomasses also resulted from deletion of the 1983 or 1985 northern pot surveys. These results reinforce a conclusion reached earlier. The relative abundance of old fish in the 1986 and 1987 fishery samples is at odds with the scarcity of old fish in the 1983 and 1985 pot index samples and with the large recent decline in the pot index.

Final Scenario

Final Model Configuration

The "final" set of runs was made with the following changes to the "preliminary" scenario. Abundances in the trawl surveys was increased by 6.5% to extrapolate to Pt. Conception. Extra juvenile natural mortality was incorporated as a parameter to be estimated and was given an initial value of 0.04, so that age 1 fish had a natural mortality of 0.19 and this rate declined exponentially to 0.15 for the older fish. Size at age 5 was adjusted to better fit the observed sizes at age 5 in the 1983 and 1985 pot index surveys. The best values for maximum size were estimated in the first set of the final scenario.

We investigated values of male maximum size in the range 62 - 68 cm (Table 8). The best fit occurred at 64 cm and we selected 64.5 cm by a crude quadratic interpolation as the value to use in the final runs. In comparing the L = 64 to the L = 68 runs, the greatest parameter change was the parameter which decreased the availability of larger males. With a smaller L , the large males are estimated to be more available. The change in likelihood for those components with substantial change was as follows: fixed gear age comp +7, trawl age comp +16, north pot survey age comp -12, fixed gear size comp +3, trawl size comp +5, trawl survey size comp +3, north pot survey size comp -3, south pot survey size comp -3, overall +14. For females, we investigated values in the range 76- 82 cm with 77.5 cm being selected as providing the best fit. At L = 78, relative to L = 82, the larger females were estimated to have higher availability to all surveys and fisheries. The change in likelihood was as follows: fixed gear age comp +2, trawl age comp +7, north pot survey age comp -7, fixed gear size comp +6, trawl size comp +1, trawl survey size comp -5, north pot survey size comp +4, south pot survey size comp +3, overall +10.

Seven final runs were made after incorporating the above changes to male and female maximum size. These runs were selected to produce an estimate of the most likely status of the west coast sablefish stock and to bracket a range of plausible alternatives. Results are summarized in Tables 10-14 and Figures 15-16. Because the extra juvenile mortality parameter was included in the set of parameters to be estimated, we tried two different starting values of virgin recruitment, 8,000 and 11,000 (Runs 1 and 2). The higher value produced a higher ending estimate for virgin recruitment (10,249 vs. 9,522) and for juvenile mortality (.042 vs. .012) and a worse fit (-1153 vs. -1143). Beginning age 3+ biomasses (174,880 vs. 175,601) and ending age 3+ biomasses (78,524 vs. 78,621) were nearly identical. The run with the starting value of 8,000 was selected as the best run to be examined in more detail below, and the following runs used a starting value of 9,500 (which was the final value from run 1) for virgin recruitment.

Increasing the emphasis on the pot index survey's abundance index (Run 3) certainly increases the goodness of fit to these observations, but degrades the fit to several types of size and age composition, especially the size composition in the northern pot index itself. This occurs for two reasons. First, the model, in an attempt to better match the fluctuations in the pot index, estimates that a narrower size range is available to the pot index thus degrading the fit to the size composition. Conversely, with a broader size (hence age) range available to the survey, the estimated survey index cannot change rapidly enough to go down to 4.8 in 1981, up to 10.6 in 1983, then decline yearly to 2.8 in 1987. Secondly, the changes in rcruitment necessary to match the index are not obvious in the size/age composition data. Overall, the fit to the northern pot index size composition in run 1 (Figure 17) was reasonably good.

Decreasing the emphasis on all age composition data causes a large degradation in the fit to the fishery age composition data (Run 4), and an improvement in the fit to all length composition data, especially the northern pot survey length composition. The fit to the pot index abundance observations is slightly degraded because, as mentioned above, a tight fit to these observations is somewhat at odds with a tight fit to the corresponding size compositions.

Natural mortality levels from 0.11 to 0.17 (Runs 5,6,7) were evaluated. Lower levels of natural mortality produce higher estimates of juvenile natural mortality, lower estimates of virgin recruitment, nearly identical starting

Table 10. Parameter values for the final runs. Pot 10x had an emphasis of 10.0 on the abundances in the northern and southern pot index. Age 0.1x had an emphasis of 0.1 on all types of age composition. Recruitments indicated as negative values were simply taken from the stock-recruitment relationship and were not individually estimated as parameters of the model. Recruitments for the year classes 1977 - 1985 were estimated as ratios to the estimated mean recruitment. Three parameters, natural mortality, trawl fishery P1, and trawl survey P1 were fixed at the indicated values and were not changed within a run.

	Start Virgin Rec				Natural Mortality		
Parameter	8000	11000	Pot 10x	Age 0.1x	M=.17	M=.13	M=.11
Nat mort	0.15	0.15	0.15	0.15	0.17	0.13	0.11
Juve mort	0.012	0.042	0.044	0.05	0.028	0.050	0.101
Male effect	1.717	1.379	1.421	1.525	1.430	1.423	1.537
Fixed P1	44.4	44.8	44.6	44.9	44.6	44.8	44.9
P2	67.2	66.4	61.5	67.5	66.9	64.8	64.2
P3	2.154	2.289	2.106	1.893	2.193	2.214	2.216
Trawl P1	36	36	36	36	36	36	36
P2	57.6	58.1	56.3	58.0	57.8	57.9	58.0
P3	4.215	4.566	5.103	4.794	4.359	4.567	4.682
Twl Svy P1	24	24	24	24	24	24	24
P2	38.3	38.1	39.4	38.7	38.1	38.5	39.0
P3	3.354	3.407	3.594	3.175	3.37	3.475	3.46
N pot P1	43.8	44.6	44.7	44.7	44.6	44.7	44.7
P2	54.2	53.3	53.3	53.9	53.4	53.2	53.4
P3	2.144	2.078	2.156	1.788	1.962	2.158	2.262
S pot P1	42.9	44.6	43.0	43.1	43.0	44.4	43.2
P2	53.4	51.9	52.5	53.6	53.2	52.1	53.1
P3	2.499	2.175	2.695	2.157	2.465	2.292	2.595
Virgin Recr.	9522	10249	9716	8947	11861	8426	7267
Mean Recr.	9560	9913	8369	9998	10143	9436	9405
Recr 69	-9283	-9952	-9415	-8628	-11593	-8153	-6997
Recr 70	-9283	-9952	-9415	-8628	-11593	-8153	-6997
Recr 71	-9283	-9952	-9415	-8628	-11593	-8153	-6997
Recr 72	-9283	-9952	-9415	-8628	-11593	-8153	-6997
Recr 73	-9254	-9923	-9382	-8598	-11553	-8125	-6979
Recr 74	-9235	-9903	-9365	-8578	-11532	-8115	-6960
Recr 75	-9197	-9863	-9323	-8528	-11482	-8077	-6932
Recr 76	-9130	-9794	-9248	-8458	-11411	-8021	-6875
Recr 77	15277	15018	12570	15156	17618	14872	14888
Recr 78	2075	3668	1306	940	2069	2076	1307
Recr 79	16854	16525	24521	15386	18389	16806	16563
Recr 80	12858	13303	10352	15126	14169	10682	10816
Recr 81	7830	7930	5892	7638	8145	8436	8088
Recr 82	8011	8396	7122	8338	8540	7662	7703
Recr 83	6214	6532	2820	10587	6258	6351	6555
Recr 84	4770	5402	3088	1320	4950	5162	4957
Recr 85	12103	12440	7791	15766	11198	12909	14004
Recr 86	-8049	-8624	-7867	-7138	-9980	-7077	-6048
Recr 87	-7906	-8465	-7574	-7018	-9737	-6983	-5991

Table 11. Likelihood values for the final runs. Where Svy indicates a survey and Fish indicates a fishery, Twl indicates trawl, Sml indicates the <42 cm component of the tri-ennial trawl survey. Twl Svy Sml Q indicates the extra component for forcing the mean deviation to be near zero. The total likelihood is the sum of the individual components weighted by the indicated emphasis factors, except using the alternate factors in the Pot 10x and the Age 0.1x runs. The standard total likelihood is computed after a run using the standard emphasis factors and zero emphasis on Twl Svy Sm Q.

		Start Virgin Rec				Natural Mortality		
Type	Emphasis	8000	11000	Pot 10x	Age 0.1x	M=.17	M=.13	M=.11
				Survey Abundance				
Twl Svy Sml	0.001	2.83	2.73	0.93	1.68	3.05	2.59	2.22
Twl Svy All	1	2.57	2.51	2.28	1.63	2.96	2.21	1.76
N Pot Svy	1(10)	-20.2	-20.7	-7.3	-22.7	-19.0	-22.3	-23.9
S Pot Svy	1(10)	-10.1	-10.4	0.0	-13.9	-7.5	-12.1	-13.8
				Age Composition				
Fix Fish	1(0.1)	-82.7	-83.1	-83.2	-138.6	-85.8	-80.9	-78.1
Twl Fish	1(0.1)	-138.7	-132.9	-160.2	-281.1	-144.4	-124.7	-119.0
N Pot Svy	1(0.1)	-135.6	-136.4	-130.4	-119.5	-139.2	-133.5	-132.8
				Size Composition				
Fix Fish	1	-66.0	-63.8	-57.7	-51.8	-62.8	-62.5	-63.5
Twl Fish	1	-48.4	-47.5	-33.2	-31.7	-44.6	-49.3	-52.3
Twl Svy	1	-191.0	-193.2	-206.8	-190.4	-190.3	-190.4	-187.7
N Pot Svy	1	-345.2	-342.7	-433.0	-282.5	-366.4	-328.6	-314.7
S Pot Svy	1	-38.1	-55.2	-37.5	-41.0	-41.0	-57.5	-42.8
				Other				
Twl Svy Sm Q	vary	-0.008	0.000	-0.013	-0.003	-0.003	-0.004	-0.010
Stock-Recr	0.001	-13.9	-4.6	-36.4	-51.6	-18.6	-13.0	-24.6
Tag Return	1	-69.7	-69.5	-77.2	-75.0	-71.7	-68.6	-67.8
Total		-1143.2	-1152.8	-1291.8	-761.5	-1169.9	-1128.3	-1095.2
Std. Total		-1143.1	-1152.8	-1224.3	-1246.6	-1169.7	-1128.2	-1094.8

Table 12. Estimates of the northern pot index for the 7 final runs: 1 = start virgin 8000, 2 = start virgin 11000, 3 = 10x pot emphasis, 4 = 0.1x age comp emphasis, 5 = natural mortality 0.17, 6 = natural mortality .13, 7 = natural mortality .11.

Final Run:		1	2	3	4	5	6	7
	Northern Pot Index							
Year	Obs	estimated						
70		10.6	10.5	11.6	11.0	11.0	10.2	9.8
71	10.3	10.5	10.4	11.5	10.9	10.9	10.1	9.8
72		10.3	10.3	11.3	10.7	10.8	9.9	9.6
73		10.1	10.1	11.1	10.5	10.5	9.8	9.4
74		9.9	9.9	10.8	10.3	10.3	9.6	9.2
75		9.6	9.7	10.5	9.9	10.0	9.3	9.0
76		9.0	9.1	9.7	9.1	9.4	8.7	8.3
77		8.5	8.6	9.1	8.6	8.9	8.2	7.9
78		8.3	8.5	8.9	8.3	8.8	8.1	7.7
79	11.4	8.0	8.1	8.2	7.8	8.4	7.7	7.4
80	6.8	7.8	7.9	7.8	7.6	8.1	7.7	7.5
81	4.8	7.7	7.8	7.9	7.4	7.9	7.7	7.6
82		7.9	7.9	8.7	7.6	7.9	8.0	8.0
83	10.6	7.9	7.8	8.4	7.7	7.7	8.0	8.1
84		7.4	7.4	7.5	7.4	7.1	7.6	7.8
85	7.4	6.7	6.7	6.2	6.9	6.3	7.0	7.3
86		6.0	5.9	4.9	6.4	5.4	6.3	6.7
87	2.8	5.5	5.5	4.0	5.8	4.9	6.0	6.4
88		5.7	5.6	3.9	6.1	4.9	6.2	6.8

Table 13. Estimates of the biomass at ages 3+ (mean within year) for the 7 final runs: 1 = start virgin 8000, 2 = start virgin 11000, 3 = 10x pot emphasis, 4 = 0.1x age comp emphasis, 5 = natural mortality 0.17, 6 = natural mortality .13, 7 = natural mortality .11.

Run:	1	2	3	4	5	6	7
Year	Biomass at Ages 3+						
70	175601	174880	162954	145019	175585	174899	174895
71	174976	174245	162198	144398	174991	174210	174155
72	172376	171957	159724	142136	172428	171835	171702
73	169049	168974	156495	139180	169187	168716	168460
74	165159	165441	152680	135673	165423	165008	164591
75	159302	159931	146843	130234	159762	159240	158580
76	146491	147420	133862	117857	147275	146295	145218
77	135798	137013	122966	107687	137057	135307	133669
78	130481	131993	117570	102703	132262	129697	127462
79	118499	120226	105235	91057	120875	117273	114344
80	117462	117973	99852	90491	120029	116570	114065
81	106553	108703	88188	79737	107373	106936	104653
82	109895	110655	99999	81788	109630	111215	109214
83	107402	107799	94316	82501	106011	107129	106180
84	100987	100883	85237	77027	97724	102507	102225
85	94512	94272	76898	72176	89715	96736	97607
86	86159	85861	63900	70171	79608	89641	91878
87	76962	77091	52198	58620	69142	81948	85046
88	78621	78524	47829	65094	67906	85474	90624

Table 14. Estimates of the fishing mortality for ages 5+ (weighted by numbers at age) for the 7 final runs: 1 = start virgin 8000, 2 = start virgin 11000, 3 = 10x pot emphasis, 4 = 0.1x age comp emphasis, 5 = natural mortality 0.17, 6 = natural mortality .13, 7 = natural mortality .11.

Run:	1	2	3	4	5	6	7
Year	Fishing Mortality at ages 5+						
70	0.023	0.023	0.025	0.028	0.023	0.023	0.024
71	0.025	0.025	0.027	0.030	0.024	0.025	0.026
72	0.043	0.043	0.047	0.052	0.043	0.044	0.045
73	0.035	0.035	0.038	0.042	0.035	0.036	0.037
74	0.053	0.053	0.058	0.064	0.053	0.054	0.055
75	0.068	0.068	0.075	0.083	0.068	0.069	0.071
76	0.166	0.167	0.187	0.206	0.166	0.170	0.172
77	0.068	0.068	0.076	0.086	0.067	0.070	0.072
78	0.104	0.104	0.116	0.132	0.102	0.107	0.110
79	0.202	0.202	0.232	0.261	0.199	0.207	0.214
80	0.081	0.080	0.094	0.106	0.079	0.082	0.085
81	0.102	0.102	0.117	0.134	0.101	0.103	0.106
82	0.168	0.168	0.187	0.221	0.168	0.171	0.175
83	0.135	0.136	0.147	0.178	0.137	0.136	0.138
84	0.138	0.139	0.167	0.177	0.142	0.138	0.140
85	0.151	0.153	0.194	0.193	0.160	0.150	0.150
86	0.153	0.154	0.211	0.192	0.165	0.149	0.147
87	0.157	0.159	0.238	0.196	0.175	0.150	0.146
88	0.126	0.128	0.199	0.156	0.144	0.119	0.114

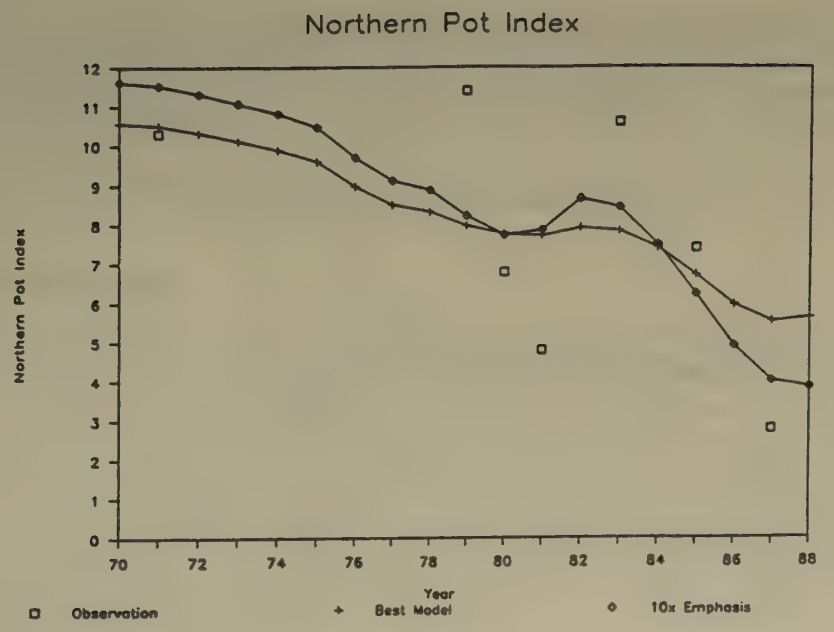


Figure 15. Northern pot index: observed and estimated.

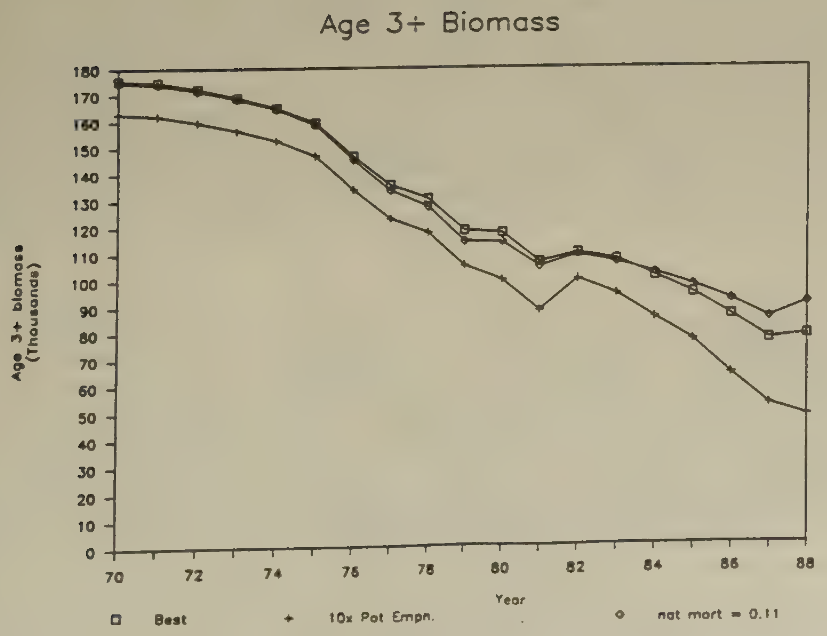


Figure 16. Biomass at age 3+ in final runs.

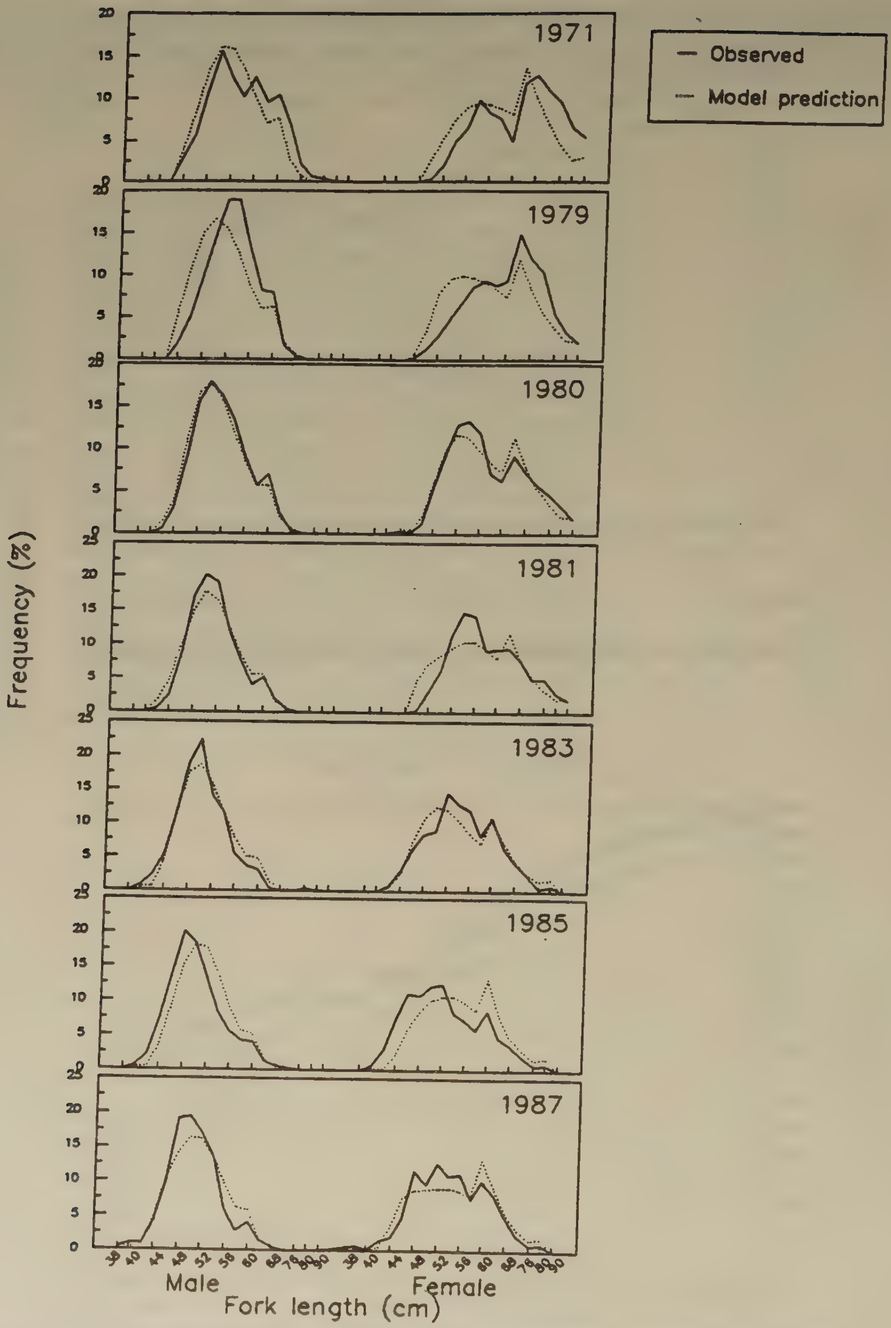


Figure 17. Time series of observed and estimated size composition in the northern pot survey. Estimated composition is from final run 1. Note variable width of size categories.

biomass levels, higher ending biomass levels, and better overall fits to the model. However, lower natural mortality seems unrealistic because of further degradation in the fit to the pot index and because of the low estimate of virgin recruitment relative to mean 1977-1985 recruitment.

The following detailed description of the model's ability to fit the data is based only on run 1 above.

Final Selectivities

The estimated selectivity patterns are described in Figures 18-19 and Table 15. Selectivity by the tri-ennial surveys is maximum at the size mode of the age 1 fish. Selectivity is similar for the two pot surveys and the trawl fishery with maximum selectivity occurring for ages 4-6. Large, old fish are most selected by the fixed gear fishery. Note that for the older fish, the two sexes are more similar in age-specific selectivity than in size-specific selectivity, especially for sizes greater than L . This is sensible for the following reason. Most of the decline in selectivity for larger older fish must be due to offshore movement, out of the range of most surveys and fisheries. The older males must tend to move offshore with similar aged females rather than remain in mid-depths with similar sized females. Because most of the pattern occurred for fish larger than L , we should in the future examine model sensitivity to the variance in size at age.

The interaction between these selectivity patterns and the normal distribution of size at age produces sample estimates of mean size at age that are biased relative to the population mean size at age (Figure 20). The tri-ennial trawl survey is relatively unbiased for the age 1 fish, the trawl fishery and pot surveys are good estimators for mean size at age 5, and the fixed gear fishery should do a good job for the age 10+ fish. A sense of the accuracy of the assumptions which lead to this result can be obtained by examining Figure 21. In 1986, the mean size of young female sablefish was overestimated in both trawl and fixed gear samples, the mean size of older female sablefish was underestimated by the predicted amount in the trawl samples, and the mean size of older female sablefish was correctly estimated by the fixed gear samples.

Deviations in Model Fit

Patterns of deviations in the fit to the diverse data are presented in Tables 16-19. An excellent fit is obtained for the tri-ennial trawl surveys (Table 16). The standard deviation of the log(observed/expected), SD, was only 0.117 for the small fish component and 0.145 for the entire size range. The model is able to obtain a good fit to these observations because each observation is composed primarily of one yearclass. Therefore, the model need adjust only one parameter (one estimated recruitment) to get a good fit to each survey. Note that for the trawl survey (small), the model is only attempting to force Q to be near 1.0 and it gives nil emphasis to year to year variations in this component.

The model is less able to fit fluctuations in the pot indexes because at least 5 ages contribute strongly to this index. The model is not able to track the two fold decline from 79 to 81, the two fold increase from 81 to 83, then the

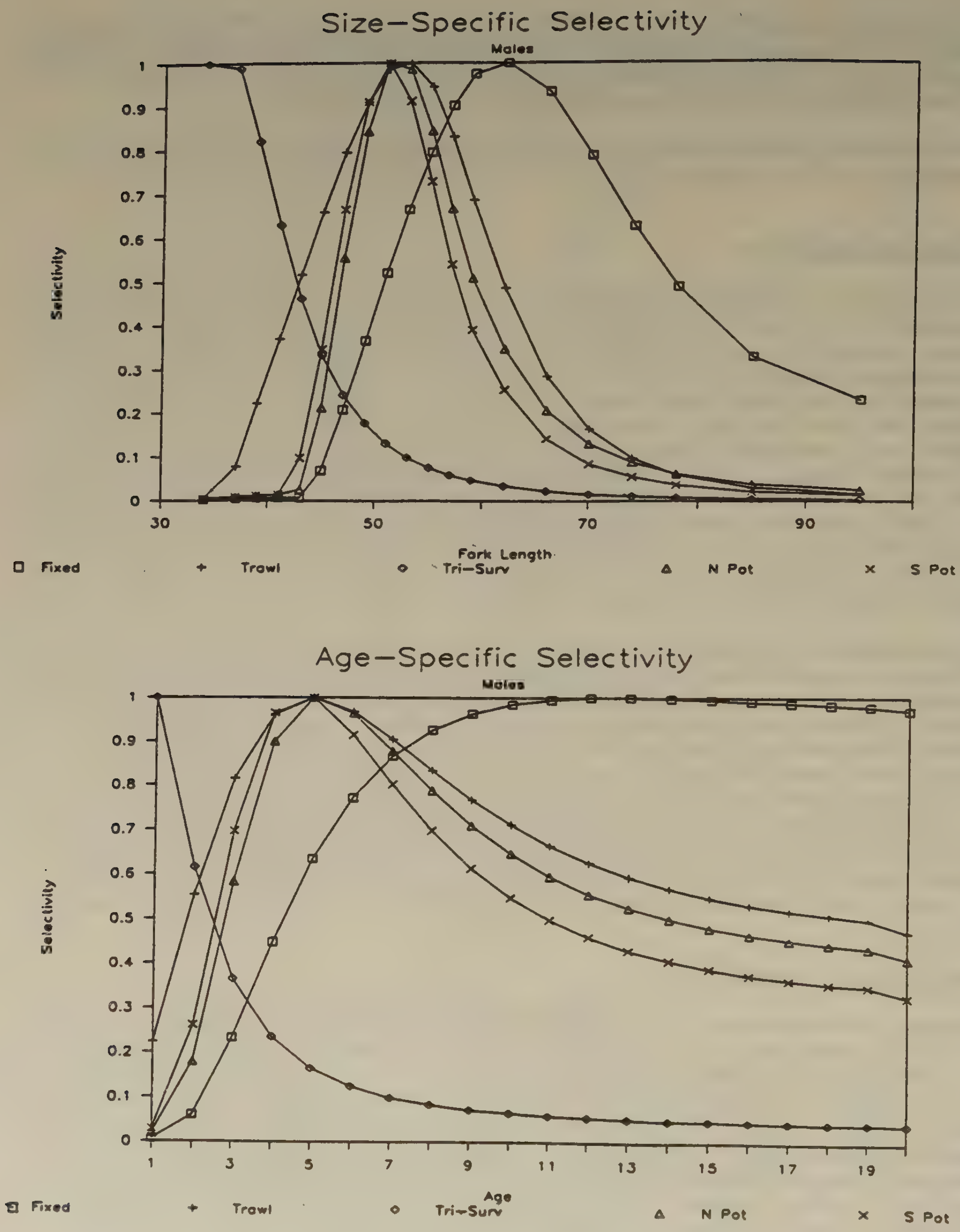
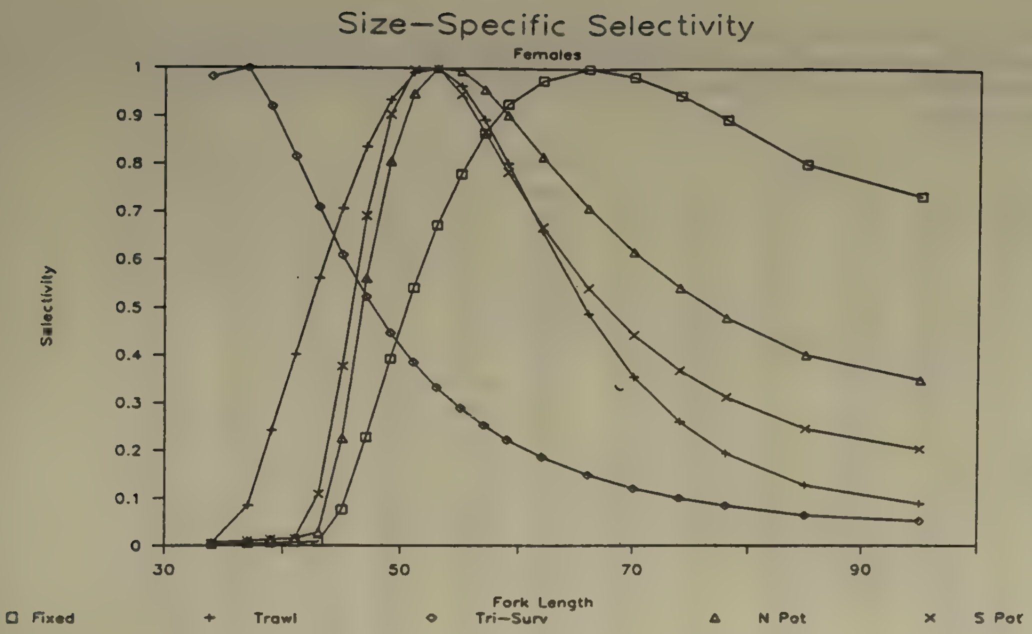


Figure 18. Size and age specific selectivity for male sablefish in the final run 1.



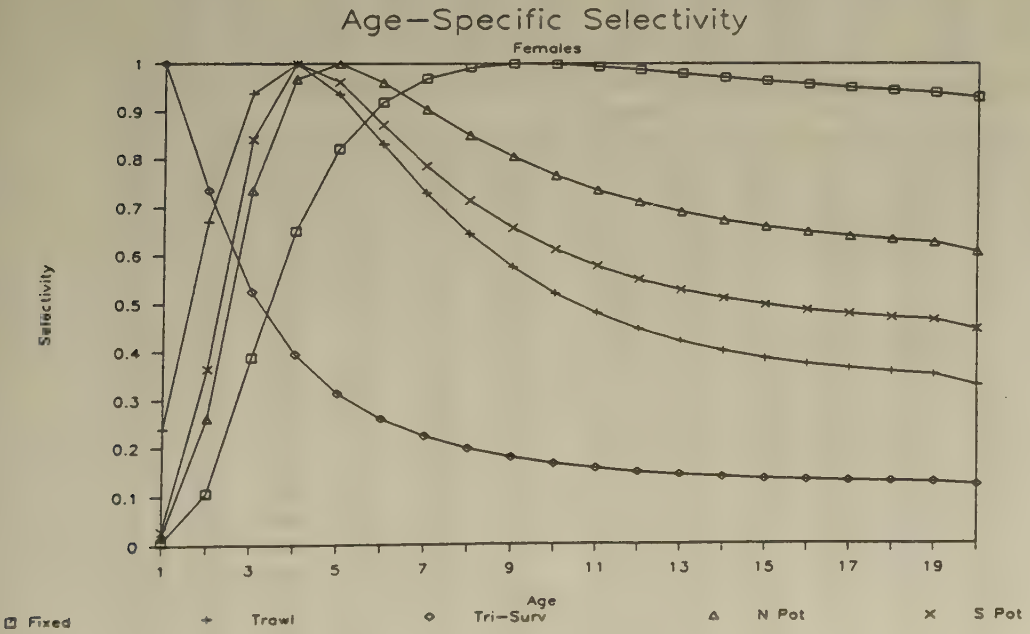


Figure 19. Size and age specific selectivity for female sablefish in the final run 1.

Table 15. Size- and age-specific selectivities in the final model. Age-specific selectivities calculated from size-specific selectivity and the distribution of size at age. Trawl retention is the same function of size for both sexes, but differs with age because of different size at age for the two sexes.

	Male					Female					Trawl
Length	Fixed	Trawl	Twl Svy	N Pot	S Pot	Fixed	Trawl	Twl Svy	N Pot	S Pot	Retain
32- 36	.002	.005	1.000	.005	.005	.002	.005	.982	.006	.006	.007
36- 38	.004	.078	.989	.009	.009	.004	.085	1.000	.010	.010	.036
38- 40	.005	.222	.821	.011	.012	.005	.243	.920	.013	.013	.152
40- 42	.006	.369	.629	.014	.014	.007	.403	.817	.015	.016	.431
42- 44	.007	.516	.461	.026	.097	.008	.561	.710	.028	.109	.755
44- 46	.069	.660	.333	.212	.346	.076	.708	.610	.226	.378	.934
46- 48	.208	.796	.241	.555	.666	.228	.837	.523	.562	.692	.986
48- 50	.366	.910	.177	.843	.911	.393	.935	.448	.807	.904	.997
50- 52	.520	.985	.131	1.000	1.000	.542	.991	.386	.947	.998	.999
52- 54	.666	1.000	.099	.985	.913	.673	1.000	.333	1.000	1.000	1.000
54- 56	.796	.945	.076	.845	.729	.780	.964	.290	.995	.946	1.000
56- 58	.903	.832	.059	.668	.541	.865	.894	.254	.957	.868	1.000
58- 60	.976	.688	.047	.509	.391	.926	.803	.223	.903	.784	1.000
60- 64	1.000	.487	.034	.347	.254	.976	.660	.187	.817	.669	1.000
64- 68	.934	.284	.023	.207	.142	1.000	.488	.149	.709	.541	1.000
68- 72	.788	.164	.016	.131	.085	.983	.356	.121	.617	.443	1.000
72- 76	.628	.097	.011	.088	.055	.944	.261	.100	.542	.369	1.000
76- 80	.489	.060	.008	.062	.037	.893	.195	.084	.480	.313	1.000
80- 90	.329	.032	.005	.039	.022	.801	.128	.064	.402	.247	1.000
90-100	.231	.017	.004	.026	.014	.736	.089	.052	.351	.205	1.000

	Male						Female					
						Trawl						Trawl
Age	Fixed	Trawl	Twl Svy	N Pot	S Pot	retain	Fixed	Trawl	Twl Svy	N Pot	S Pot	retain
1	.006	.223	1.000	.019	.028	.384	.007	.239	1.000	.018	.028	.383
2	.060	.554	.616	.179	.261	.767	.106	.670	.736	.262	.365	.834
3	.233	.815	.366	.584	.697	.935	.388	.938	.526	.736	.842	.969
4	.448	.961	.235	.900	.965	.982	.651	1.000	.395	.968	1.000	.993
5	.634	1.000	.164	1.000	1.000	.994	.822	.936	.313	1.000	.961	.998
6	.772	.968	.124	.964	.915	.998	.919	.832	.260	.960	.872	.999
7	.867	.905	.099	.878	.802	.999	.969	.730	.224	.904	.786	1.000
8	.927	.834	.083	.788	.699	.999	.992	.645	.198	.850	.714	1.000
9	.964	.768	.072	.710	.614	1.000	1.000	.576	.180	.805	.657	1.000
10	.985	.712	.065	.647	.549	1.000	.999	.521	.166	.766	.612	1.000
11	.995	.664	.059	.596	.499	1.000	.994	.479	.156	.735	.577	1.000
12	1.000	.626	.055	.556	.460	1.000	.987	.446	.148	.710	.549	1.000
13	1.000	.594	.052	.525	.430	1.000	.979	.420	.142	.689	.527	1.000
14	.998	.569	.049	.501	.408	1.000	.971	.400	.137	.672	.510	1.000
15	.995	.549	.048	.481	.390	1.000	.964	.385	.133	.659	.497	1.000
16	.991	.532	.046	.466	.376	1.000	.957	.373	.131	.648	.486	1.000
17	.987	.519	.045	.454	.365	1.000	.950	.364	.129	.639	.478	1.000
18	.983	.509	.044	.445	.357	1.000	.944	.357	.128	.632	.471	1.000
19	.979	.500	.044	.437	.351	1.000	.939	.351	.127	.626	.466	1.000
20	.971	.474	.042	.414	.329	1.000	.929	.329	.121	.607	.446	1.000

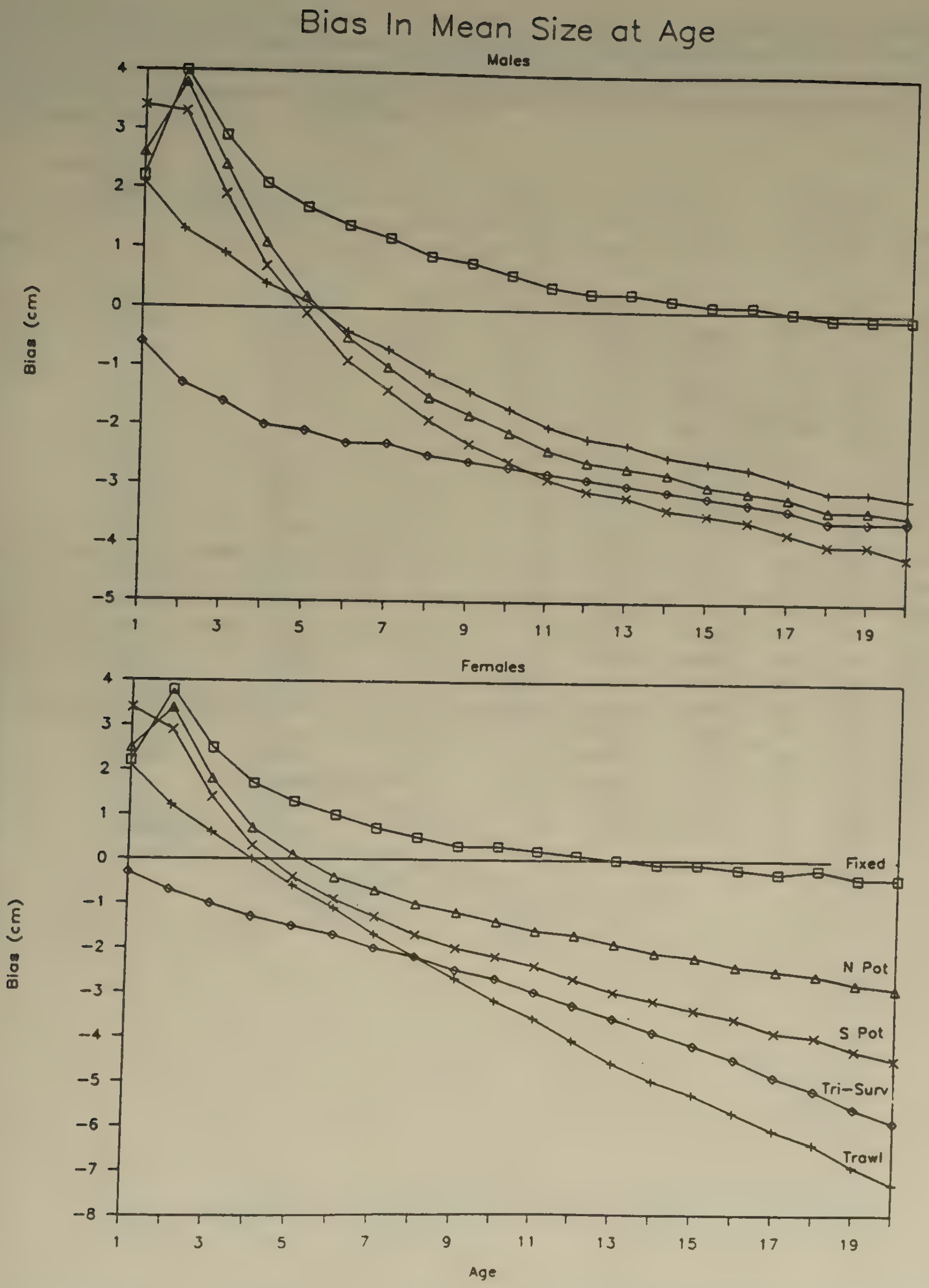


Figure 20. Calculated bias in mean size at age for each type of sampler.

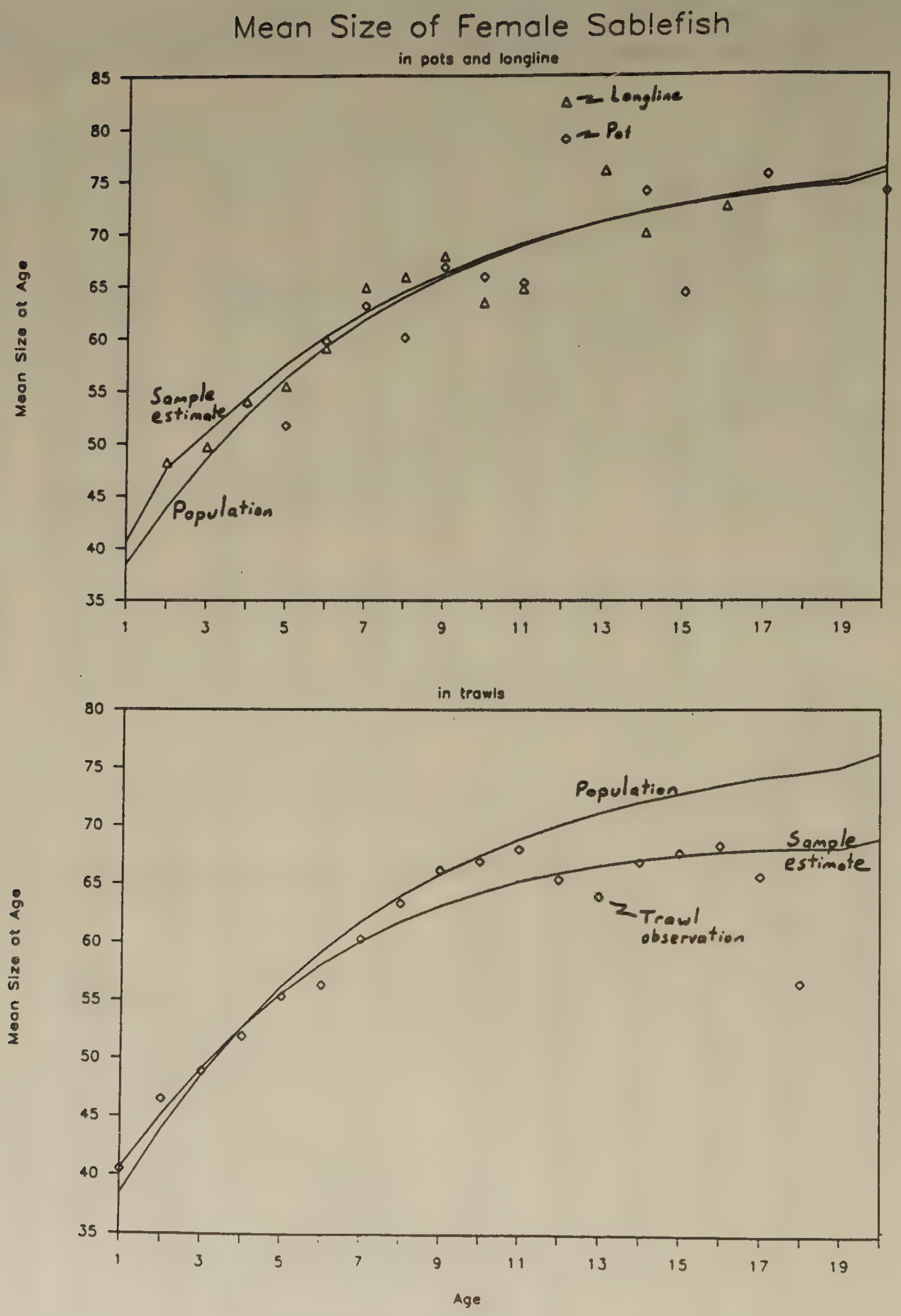


Figure 21. Estimated and observed mean size at age for female sablefish in the 1986 fishery.

Table 16. Results of the final model run including: observed and estimated values for each type of survey; mean biomass within each year, fishing mortality for the age at selectivity = 1.0; and estimated biomass discarded by the trawl fishery. Q is the ratio of the mean observed to the mean estimated. MN is the mean of the log(observed/estimated). SD is the standard deviation of the log(observed/estimated).

	Trawl Survey												
	< 42 cm		all sizes		N Pot		S Pot		Biomass		F at Full - Selection-		Trawl
Year	Obs	Est	Obs	Est	Obs	Est	Obs	Est	Total	Age 3+	Fixed	Trawl	Discard
70		21600.		44918.		10.6		11.1	195162.	175473.	.009	.020	77.
71		21441.		44489.	10.3	10.5		11.0	194200.	174845.	.011	.021	78.
72		21379.		44043.		10.3		10.8	191554.	172243.	.024	.030	110.
73		21343.		43653.		10.1		10.6	188188.	168914.	.013	.034	124.
74		21300.		43298.		9.9		10.4	184274.	165023.	.037	.027	101.
75		21244.		42852.		9.6		10.1	178360.	159165.	.050	.032	115.
76		21100.		41794.		9.0		9.5	165413.	146353.	.156	.036	129.
77		20978.		41107.		8.5		9.1	154633.	135659.	.045	.039	140.
78		31168.		51906.		8.3		8.9	154739.	130341.	.065	.064	291.
79		11973.		32862.	11.4	8.0		8.7	137460.	118359.	.157	.085	281.
80	34349.	30686.	53418.	49469.	6.8	7.8		8.4	135096.	117320.	.052	.047	187.
81		30530.		52114.	4.8	7.7		8.5	137399.	106415.	.060	.066	330.
82		20790.		43087.		7.9		8.8	131225.	109757.	.087	.121	504.
83	17972.	18420.	40573.	38299.	10.6	7.8		8.6	123266.	107264.	.075	.093	312.
84		15101.		32663.		7.4	9.8	8.1	115424.	100851.	.060	.111	316.
85		11747.		26871.	7.4	6.7		7.2	105614.	94375.	.080	.105	239.
86	20519.	23150.	30856.	37080.		6.0	4.6	6.3	102332.	86027.	.083	.105	324.
87		19879.		35329.	2.8	5.5		6.0	97610.	76840.	.087	.106	364.
88		18209.		34042.		5.6		6.3	94706.	78501.	.071	.085	272.
89		17676.		33202.		5.8		6.4	93178.	77232.	.072	.085	258.
90		17402.		32582.		5.7		6.3	91651.	75972.	.073	.085	253.
91		17222.		32110.		5.7		6.2	90098.	74590.	.074	.086	252.
Q	.99		.87		5387.59		4831.30						
MN	-.011		-.016		-.08		-.06						
SD	.117		.145		.39		.37						

Table 17. Observed and estimated tag returns. Estimated returns are calculated from the time series of F and Z for ages 5+ in the years following the release. For presentation, the expected proportion of returns in each subsequent year is multiplied by the total number of tags actually returned from that release.

Release				Returns in Year											
Year	F	Z		77	78	79	80	81	82	83	84	85	86	87	Sum
76	.167	.317	E:	50	55	72	19	17	19	10	7	5	3	2	
			O:	30	38	85	16	22	32	21	7	6	3	4	264
77	.068	.218													
78	.104	.254													
79	.202	.352	E:				24	21	24	13	9	6	4	3	
			O:				26	26	20	10	9	10	2	4	107
80	.081	.231	E:					120	134	72	50	37	25	17	
			O:					121	104	137	26	27	32	10	457
81	.102	.252	E:						51	27	19	14	9	6	
			O:						57	27	8	16	16	4	128
82	.168	.318	E:							17	12	9	6	4	
			O:							23	7	6	10	3	49
83	.135	.285	E:								5	4	2	1	
			O:								5	5	2	2	14
84	.138	.288													
85	.152	.302													
86	.153	.303	E:											54	
			O:											54	54
87	.157	.307													

Table 18. Deviations in age composition for the final run. Types are: 1 fixed gear fishery, 2 - trawl fishery, 5 - northern pot survey. LIKE/FISH is the likelihood for that type of data divided by the total number of fish aged.

			--- MEAN AGE --			
YEAR	TYPE	SEX	OBSERV	EXPECT	DEVIATE	LIKE
83	5	1	4.86	5.30	-.44	-9.46
83	5	2	4.94	5.32	-.38	-49.16
85	5	1	5.02	5.61	-.59	-31.41
85	5	2	4.60	5.66	-1.06	-45.49
86	1	1	7.32	6.93	.39	-2.08
86	1	2	6.67	6.65	.03	-3.48
86	2	1	6.16	5.41	.76	-21.26
86	2	2	5.00	4.99	.01	-9.92
87	1	1	8.47	6.98	1.48	-45.61
87	1	2	7.99	6.66	1.34	-31.68
87	2	1	6.48	5.18	1.31	-81.74
87	2	2	5.13	4.66	.47	-26.01

TYPE	SEX	MEAN DEVIATE	LIKE/ FISH
1	1	.93	-.13
1	2	.68	-.08
2	1	1.03	-.13
2	2	.24	-.04
5	1	-.52	-.06
5	2	-.72	-.13

Table 19. Deviations in size composition in the final run. Types are: 1 fixed gear fishery, 2 - trawl fishery, 4 - trawl survey, 5 - northern pot survey, 6 - southern pot survey.

			— MEAN LENGTH —			
YEAR	TYPE	SEX	OBSERV	EXPECT	DEVIATE	LIKE
71	5	1	55.36	53.52	1.83	-30.51
71	5	2	63.11	59.23	3.88	-44.44
79	5	1	54.24	52.81	1.43	-33.38
79	5	2	60.89	57.82	3.07	-34.89
80	4	1	41.19	40.58	.61	-23.91
80	4	2	42.89	43.84	-.95	-52.78
80	5	1	53.19	52.63	.55	-3.85
80	5	2	57.94	57.61	.33	-7.09
81	5	1	52.78	52.63	.16	-8.30
81	5	2	58.45	57.49	.96	-31.08
83	4	1	42.31	42.02	.29	-12.56
83	4	2	44.22	45.78	-1.55	-29.88
83	5	1	51.42	52.28	-.86	-14.15
83	5	2	56.40	56.77	-.36	-11.07
84	6	1	51.50	51.65	-.15	-2.53
84	6	2	56.12	55.68	.45	-12.14
85	5	1	51.41	52.78	-1.36	-34.35
85	5	2	54.29	57.69	-3.40	-61.85
86	1	1	56.03	56.71	-.68	-19.91
86	1	2	60.07	61.76	-1.69	-14.76
86	2	1	52.37	52.01	.36	-7.45
86	2	2	53.20	54.63	-1.42	-13.14
86	4	1	40.44	40.63	-.20	-10.11
86	4	2	46.31	43.97	2.35	-61.74
86	6	1	51.42	52.05	-.63	-12.00
86	6	2	56.92	56.47	.46	-11.38
87	1	1	56.05	56.75	-.71	-15.63
87	1	2	61.93	61.71	.22	-15.69
87	2	1	50.68	51.45	-.77	-6.43
87	2	2	51.69	53.55	-1.86	-21.25
87	5	1	51.98	52.77	-.79	-16.34
87	5	2	56.58	57.63	-1.05	-13.86

		MEAN DEVIATE	LIKE/ FISH
1	1	-.70	-.04
1	2	-.74	-.04
2	1	-.21	-.02
2	2	-1.65	-.04
4	1	.23	-.04
4	2	-.06	-.13
5	1	.14	-.05
5	2	.49	-.08
6	1	-.39	-.02
6	2	.45	-.03

Table 20. Recruitment deviations for the final model. Q is the ratio of the mean estimate to the mean expected. MN is the mean of the log(estimate/expect). SD is the standard deviation of log(estimate/expect).

Virgin spawning biomass = 102686.6 mt of females
Virgin recruitment = 9522.4 thousand per sex
Density-dependence = 0.889

Year-class	Estimate	Expect	Ratio
77	15277.	8929.	.54
78	2075.	8874.	-1.45
79	16854.	8776.	.65
80	12858.	8525.	.41
81	7830.	8488.	-.08
82	8011.	8436.	-.05
83	6214.	8296.	-.29
84	4770.	8221.	-.54
85	12103.	8154.	.39

Q = .892 MN = -0.047 SD = .663

three fold decline from 83 to 87. With higher emphasis on the pot index the model achieves somewhat better tracking (Figure 15), but the SD for the pot index remains above 0.3 as compared to the average coefficient of variation, 0.16, for the 1983, 1985 and 1987 northern pot indexes. The northern and southern pot index are surprisingly similar. They have similar size-specific selectivity patterns (Figures 18-19), similar catchability coefficients, Q, 5388 vs. 4831, and the downward trend from 83-87 seems even more apparent when the two surveys are plotted together (Figure 9). The observed fluctuations in the pot index have shown good coherence along the coast, so changed distribution probably has not caused the fluctuations and the real cause remains an enigma. With the moderately strong 1985 year class entering the size range available to the pot index, the model predicts a leveling off of the pot index values. A southern pot survey is tentatively scheduled for autumn of 1988; the model predicts that the index value will be 6.3 (approximate 95%CI based on SD=0.37 is 3.0 - 13.2).

The pattern of tag returns was well matched by the model (Table 17). The largest deviation occurred for tags released in 1980 and returned in 1983, the returns were nearly twice the expected. Overall there were no obvious patterns to the deviations.

Patterns in the age and size composition data are more difficult to display becuase of the great volume of data (Table 18-19).. The model underestimates mean age and overestimate mean size in the fishery samples, especially in 1987. Mean age is overestimated for the northern pot survey samples and mean size is underestimated in these samples, especially in the early years. There are no age composition data for the trawl survey or the southern pot index and the fit to the size composition data from these surveys seems unbiased. The log likelihood for each type of age or size composition data depends on the number of observations and the number of fish per observation. When the log likelihoods are divided by the total number of fish, we see that the size compositions are fit more precisely than the age compositions and that male size compositions tend to be fit more precisely than female size compositions.

Fit to the spawner-recruitment relationship is given nil weighting in the model, but patterns of deviations still contribute to our understanding of what has happened to the sablefish stock (Table 20). As spawning biomass has decreased, the model predicts that recruitments should have declined from 8929 thousand in 1977 to 8154 thousand in 1985. However, the model estimates that recruitment was better than expected in 1977, 1979, 1980, and 1985. Average recruitments occurred in 1981 and 1982. Poor recruitments occurred in 1978, 1983 and 1984.

The estimated sablefish population at the beginning of 1988 is presented in Table 21. These values and the estimated selectivity functions are used below to forecast the near term changes in the stock and stock equilibrium as a function of different levels of fishing effort.

Table 21. Estimated population at the beginning of 1988 in the final run.

	MALES			FEMALES		
AGE	NUMBERS	BIOMASS	Z	NUMBERS	BIOMASS	Z
1	7908.9	3938.7	.181	7908.9	3938.7	.182
2	6683.0	4789.3	.206	6671.0	5215.3	.219
3	8083.9	7629.8	.237	7938.9	8757.6	.259
4	2463.0	2876.6	.264	2356.1	3404.9	.282
5	2400.0	3314.3	.280	2248.3	4031.8	.288
6	2280.0	3597.3	.287	2119.3	4527.2	.286
7	1629.9	2862.0	.288	1524.5	3758.8	.281
8	1973.1	3777.5	.286	1866.6	5181.2	.275
9	1946.3	3997.6	.283	1877.6	5751.7	.269
10	183.2	398.5	.280	181.5	603.8	.265
11	1037.9	2366.3	.277	1048.6	3738.1	.261
12	479.7	1136.7	.274	489.3	1849.2	.258
13	377.2	922.5	.271	390.9	1551.9	.255
14	299.4	751.8	.269	315.7	1307.2	.253
15	237.7	609.9	.267	253.4	1086.8	.251
16	190.0	496.2	.265	205.3	907.7	.249
17	153.1	406.0	.264	168.5	764.4	.248
18	125.3	336.2	.263	140.7	652.4	.247
19	103.9	281.8	.262	119.1	562.5	.246
20	614.3	1710.2	.259	747.4	3727.2	.243

TOTAL N	77741.
TOTAL BIOMASS	107518.
SPAWNING BIOMASS	33532.
AGE 3+ BIOMASS	89636.

Yield Projections

Results from the synthesis model were used to estimate equilibrium yield and stock size for a range of levels of fishing mortality. Following Getz (1980), we calculated the equilibrium number-at-age vectors at each level of F by defining the equilibrium spawning stock as a function of the number of age-1 females, N_1:

$$
\begin{aligned}
SPB &= \underset{a}{\hat{E}} [N_a * PCTMAT_a * W_{a2}] \\
&= [N_1 * PCTMAT_1 * W_{1,2}] \\
&\quad + N_1 * \overset{19}{\underset{a=2}{\hat{E}}} \left| PCTMAT_a * W_{a2} * \overset{a-1}{\underset{J=1}{}} e^{(-M_j - F_j)} \right| \\
&\quad + N_1 * PCTMAT_{20} * W_{20,2} * \\
&\quad \overset{19}{\underset{J=1}{}} e^{(-M_j - F_j)} / (1 - e^{(-M_{20} - F_{20})}) \\
&= N_1 * SPSUM
\end{aligned}
$$

By substituting N_1*SPSUM for SPB in the stock-recruitment relationship and solving for N_1, the number of recruits was expressed as a function of F:

$$N_1 = VSPB * (VR * SPSUM/VSPB + DD - 1)/\ (DD * SPSUM)$$

The numbers at age 1 for males is assumed to be the same as the numbers for females. The number of fish ages 2-20 was calculated from the number at age 1. Equilibrium yield was calculated from the catch equation described earlier except that weight of age-A fish in the catch was obtained from the length-weight relationship using the estimated mean length of age-A, sex-S fish captured by gear type T.

We calculated equilibrium number-at-age vectors and associated yields for a range of trawl and fixed gear F combinations. The resulting matrix of yield values was used to produce response surface plots, with plot contours representing levels of equilibrium yield or the percentage of total yield due to trawl gear (Figures 22-25). The shape and elevation of the response surface for total yield was similar for the seven cases examined, but substantially different for the constant (DD=1.000) and Beverton-Holt (DD=0.889) stock-recruitment cases. As in an earlier study (Francis 1985), highest yields were obtained when fishing was limited to fixed gear vessels (Figures 22, 24). Compared to a fixed gear only fishery, MSY for the Beverton-Holt case was 929 to 1,035 mt lower for the seven cases examined when a 52:48 trawl:fixed gear allocation was maintained. Note that this change in yield may provide an upper bound for the increase in yield that might be obtained by increasing trawl mesh size.

We also calculated equilibrium yield at different total Fs by solving iteratively for the trawl and fixed gear Fs that would result in a 52:48 trawl:fixed

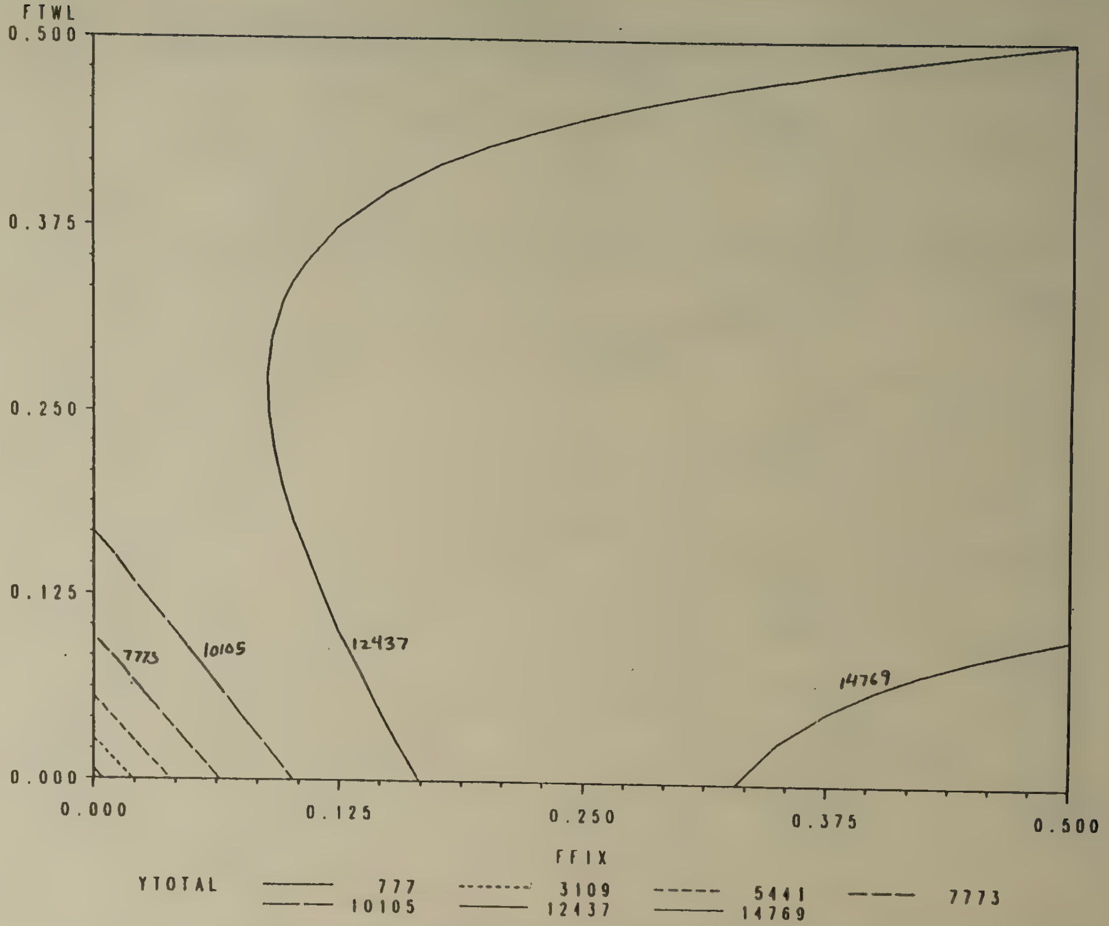


Figure 23. Total yield for various combinations of trawl and fixed gear Fs, using parameter estimates from stock synthesis model run 1, assuming constant recruitment (A=1.000).

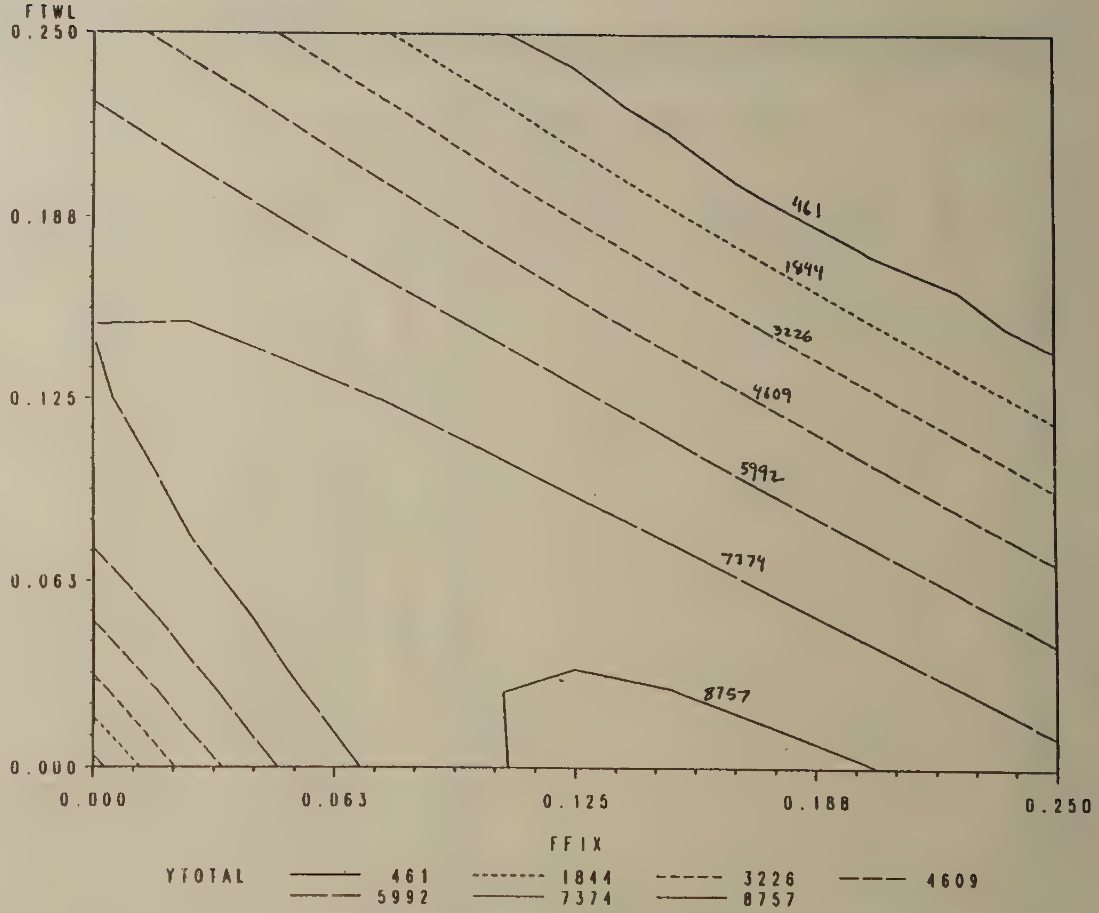


Figure 22. Total yield for various combinations of trawl and fixed gear Fs, using parameter estimates from stock synthesis model run 1.

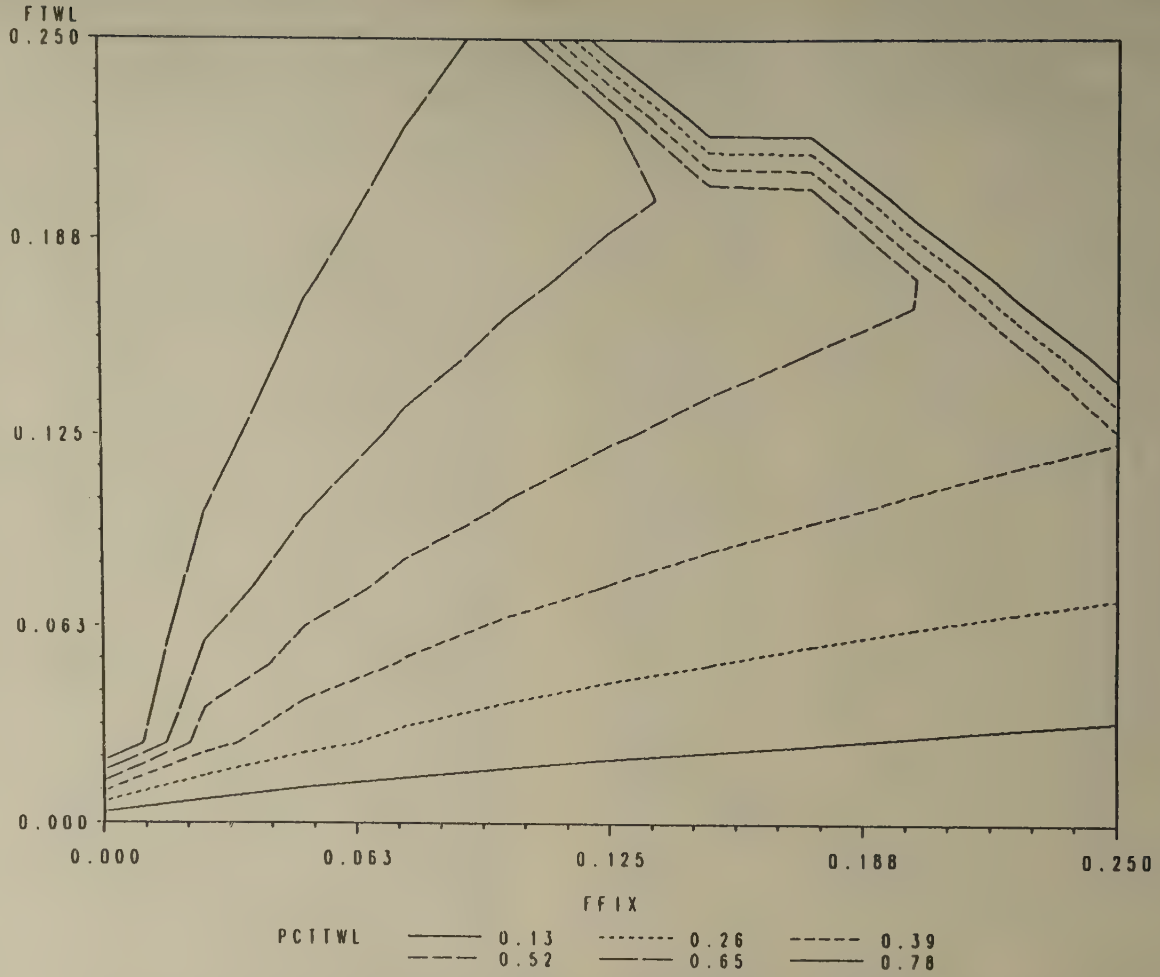


Figure 24. Percentage of total yield due to trawl gear for various combinations of trawl and fixed gear Fs, using parameter estimates from stock synthesis model run 1.

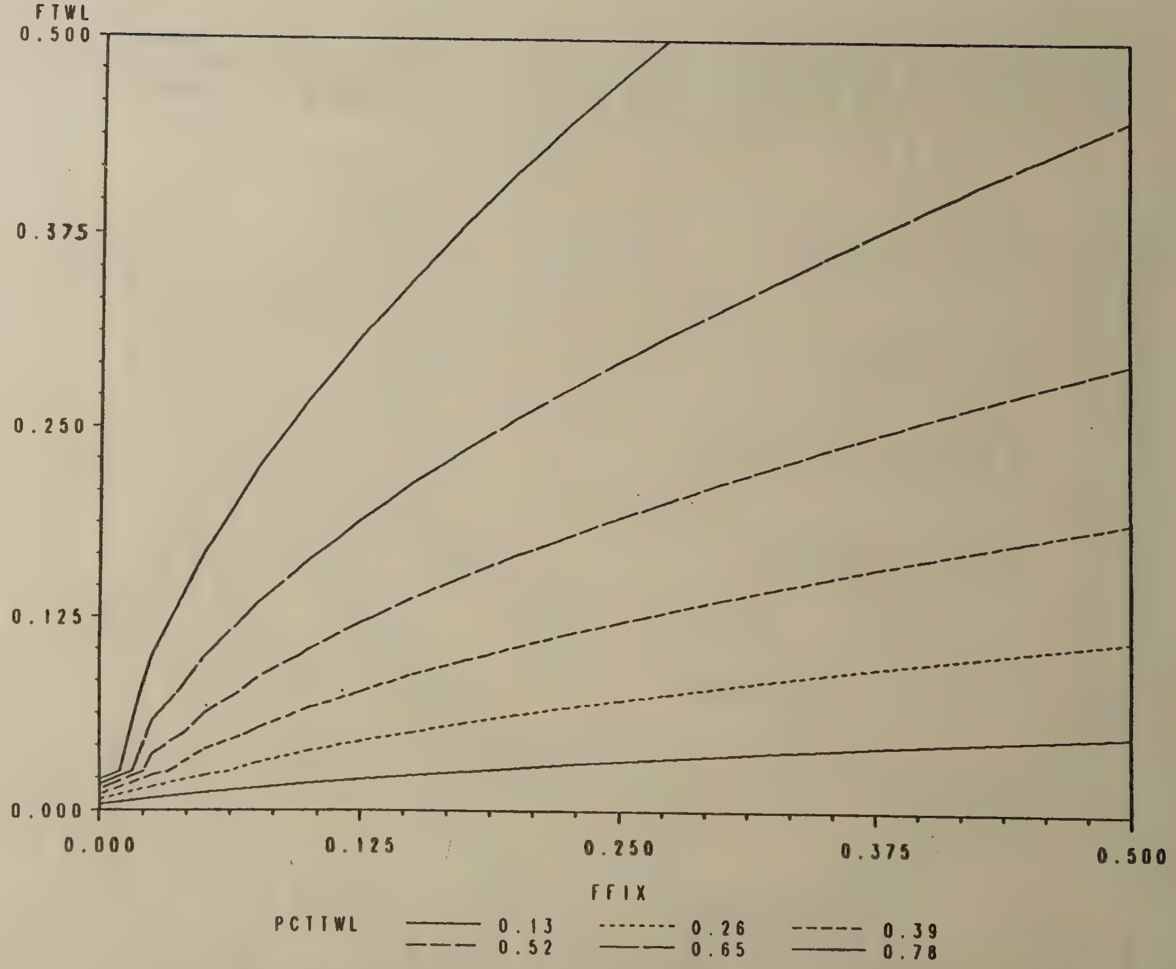


Figure 25. Percentage of total yield due to trawl gear for various combinations of trawl and fixed gear Fs, using parameter estimates from stock synthesis model run 1, assuming constant recruitment (A=1.000).

gear allocation (Figures 26). Yield and stock biomass curves for the seven cases were similar in shape and in magnitude. Yield curves for the two stock-recruitment cases differed considerably, with total yield about 3-4 thousand mt higher under the optimistic constant recruitment assumption. Following Francis (1986), we assumed that F[MSY] and F[0.1] were appropriate Fs for the Beverton-Holt (DD=0.889) and constant recruitment cases (DD=1.000) respectively. For each stock-recruitment case, recommended Fs and yields were similar for the seven cases examined (Tables 22-23). For the density-dependent case, recommended total Fs (F[MSY]) were relatively low (0.11-0.14; less than M in 6 of 7 cases). These conservative results apparently were obtained because of the early age at first recruitment, relative to age at first maturity. When constant recruitment was assumed, recommended total Fs were substantially higher (0.16-0.21 for females). In both cases, recommended Fs were lowest for M=0.11 and highest for the M=0.15 and M=0.17 cases. For the Beverton-Holt case, recommended equilibrium yields ranged from 6,988 to 9,162 mt. For the constant recruitment case, recommended yields ranged from 9,831 to 13,607 mt. Biomass levels at the recommended Fs were similar for all cases examined.

Using the current 52:48 trawl:fixed gear allocation, we solved iteratively for the trawl and fixed gear Fs required to obtain constant catches of 8,000 to 12,000 mt from 1988 through 1992 (Tables 24-25). These Fs can be used to compare the predicted short-term impact of alternative ABC levels. For the Beverton-Holt case, the required Fs change slowly over a 5-year horizon except in cases where the target harvest greatly exceeded MSY (e.g. 12,000 mt harvest for run 3). For the constant recruitment case, required Fs varied only slightly over the 5-year horizon.

We obtained estimates of ABC by assuming a 1988 harvest of 10,000 mt and a constant F in 1989-1990 equal to either F[MSY] (DD=0.889) or F[0.1] (DD=1.000). For a specified total F, we solved iteratively for the trawl and fixed gear Fs that would result in a 52:48 trawl:fixed gear allocation. For runs 1, 2, 6, and 7 the total biomass in 1988 is 8,000 - 16,000 mt greater than the biomass at MSY. For run 5 (natural mortality = .17) the current stock is essentially right on the biomass yielding MSY. For runs 3 and 4 (high pot emphasis or low age composition emphasis) the current biomass is below that producing MSY. Predicted 1989-1990 biomass levels were similar for most cases examined; the lowest estimates were for the cases where the relative importance of the pot survey data was increased (Tables 26-27). For each stock-recruitment case, differences in 1989-1990 yield were due mostly to differences in the starting biomass level. Note that the biomass in 1988 is inversely related to the assumed level of natural mortality and that the F[MSY] is positively related to the assumed level of natural mortality (Table 22). The combination of these two factors produces maximum ABC at an intermediate level of natural mortality, 0.15. There were substantial differences in 1989-1990 yield for the two stock-recruitment cases, due to the differences in F[MSY] and F[0.1].

The stock could be fished down to the B[MSY] level more or less rapidly than the rate indicated by applying F[MSY] to the current stock. Table 28 presents various fishing down scenarios. Here we have set the 1988 total catch at 10,800 mt because of the recently released reserve. If the ABC in 1989 was set equal to 15,400 mt then the B[MSY] level would be reached the following year. However, this would be a risky policy and would result in substantial over-fishing if our assessment has over-estimated sablefish abundance.

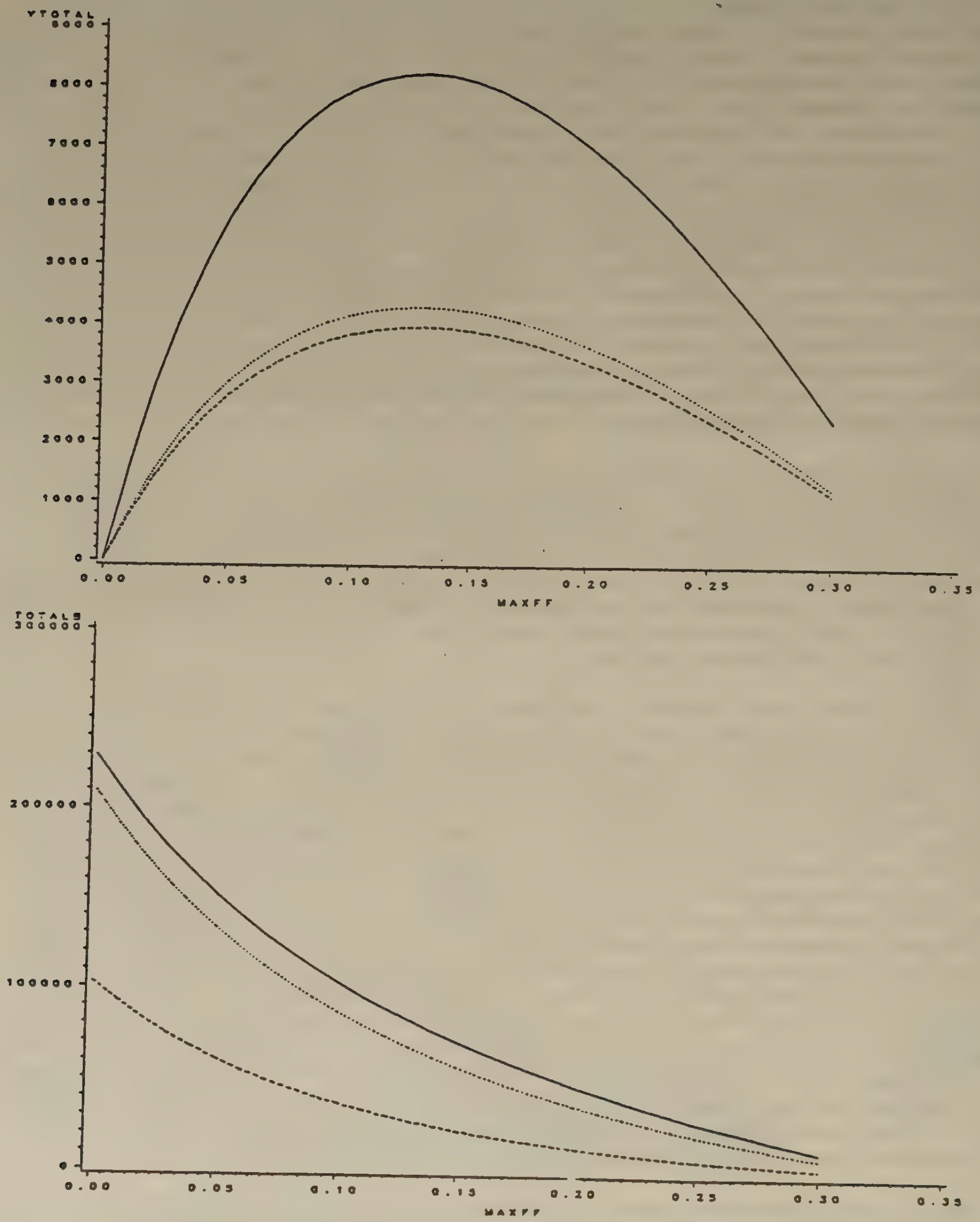


Figure 26. Upper panel: Equilibrium total (solid line), trawl (dotted line), and fixed gear (dashed line) yields as a function of maximum age-specific F for females (Fs for females and males were essentially equivalent). Lower panel: Equilibrium total (solid line), exploitable (ages 3+, dotted line), and female spawning (dashed line) biomass as a function of maximum age-specific F for females. A 52:48 trawl:fixed gear allocation was assumed.

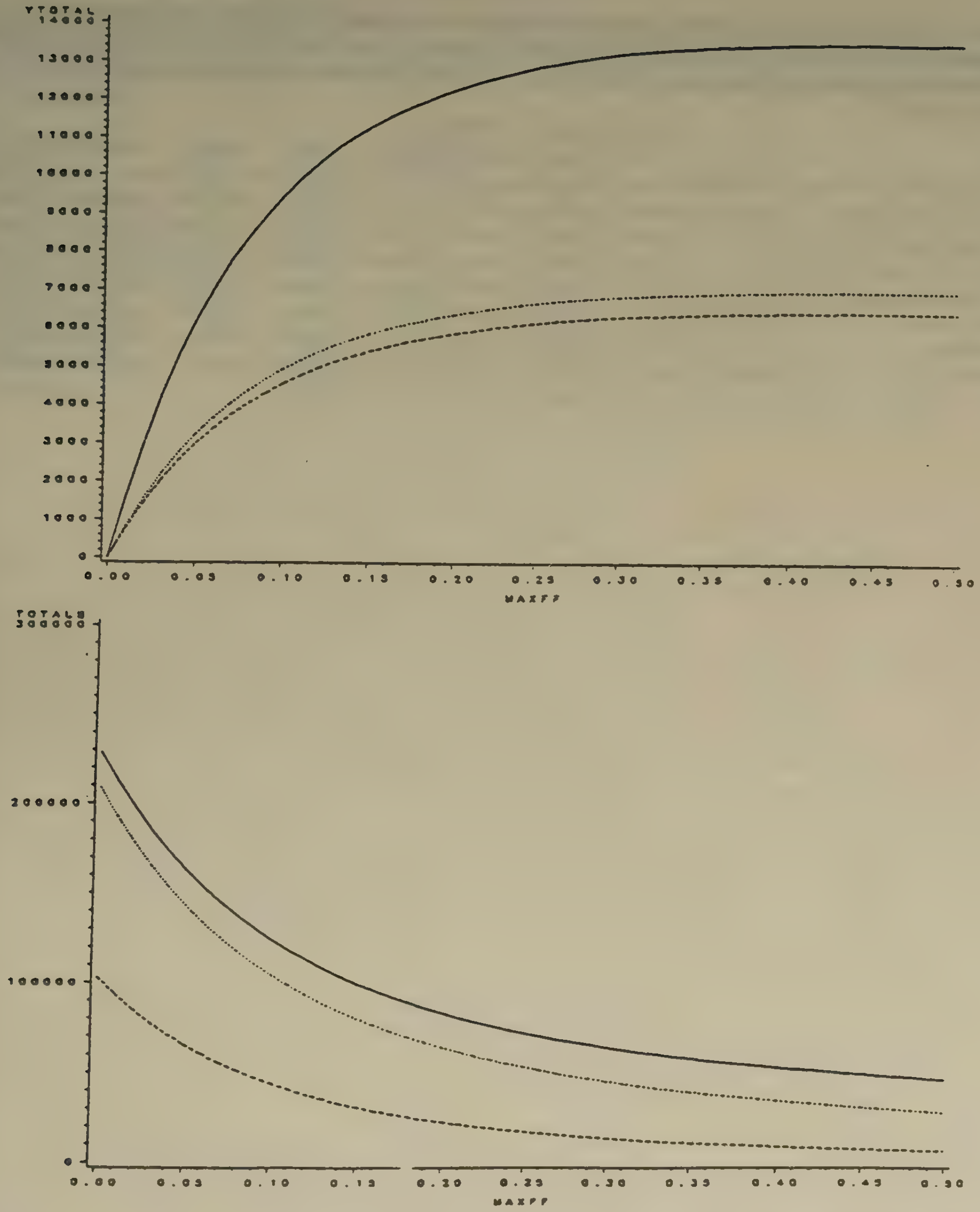


Figure 27. Upper panel: Equilibrium total (solid line), trawl (dotted line), and fixed gear (dashed line) yields as a function of maximum age-specific F for females, assuming constant recruitment (A=1.000). Lower panel: Equilibrium total (solid line), exploitable (ages 3+, dotted line), and female spawning (dashed line) biomass as a function of maximum age-specific F for females, assuming constant recruitment (A=1.000). A 52:48 trawl:fixed gear allocation was assumed.

Table 22. Estimates of MSY, F[MSY], and equilibrium stock biomass levels for seven sets of assessment parameters. The total F[MSY] estimate for each sex is the highest age-specific F, rather than the sum of trawl and fixed gear F multipliers, because the age at full recruitment differs for the two gears.

		F multiplier		Total F					
Run	R1	FIX	TWL	Female	Male	MSY	B[MSY]	S[MSY]	B[MSY,3+]
1 (best, start=8000)	9,522	0.069	0.079	0.130	0.131	8,198	82,676	26,990	67,804
2 (best, start=11000)	10,250	0.068	0.078	0.130	0.131	8,570	87,967	28,853	71,999
3 (10X pot surv abund)	9,716	0.068	0.088	0.140	0.144	7,849	78,330	25,842	63,563
4 (0.1X all age comp)	8,947	0.071	0.081	0.130	0.134	7,454	74,897	24,423	61,112
5 (M=0.17)	11,861	0.077	0.082	0.140	0.141	9,162	87,404	26,143	69,307
6 (M=0.13)	8,426	0.059	0.074	0.120	0.121	7,695	85,848	30,948	72,461
7 (M=0.11)	7,267	0.051	0.070	0.110	0.112	6,988	86,475	34,072	74,918

Table 23. Estimates of Y[0.1], F[0.1], and equilibrium stock biomass levels for seven sets of assessment parameters. The total F[0.1] estimate for each sex is the highest age-specific F, rather than the sum of trawl and fixed gear F multipliers, because the age at full recruitment differs for the two gears.

		F multiplier		Total F					
Run	R1	FIX	TWL	Female	Male	Y[0.1]	B[0.1]	S[0.1]	B[0.1,3+]
1 (best, start=8000)	9,522	0.107	0.109	0.190	0.191	12,170	86,083	23,890	66,871
2 (best, start=11000)	10,250	0.106	0.108	0.190	0.192	12,486	89,811	25,052	69,626
3 (10X pot surv abund)	9,716	0.110	0.125	0.210	0.217	11,706	78,067	21,356	59,170
4 (0.1X all age comp)	8,947	0.112	0.112	0.190	0.196	10,866	76,656	21,202	59,171
5 (M=0.17)	11,861	0.123	0.116	0.210	0.212	13,607	89,970	22,322	66,898
6 (M=0.13)	8,426	0.095	0.105	0.180	0.182	11,199	84,211	25,842	67,378
7 (M=0.11)	7,267	0.079	0.097	0.160	0.162	9,831	83,304	28,744	69,073

Table 24. Total F for female sablefish required to obtain yields of 8,000 to 12,000 mt in 1988-1992, assuming a Beverton-Holt stock recruitment relationship (A=0.889).

	Yield	Year				
Run	(mt)	1988	1989	1990	1991	1992
1 (best, start=8000)	8,000	0.112	0.110	0.109	0.108	0.108
	9,000	0.127	0.126	0.126	0.127	0.128
	10,000	0.142	0.143	0.145	0.147	0.150
	11,000	0.157	0.160	0.164	0.169	0.175
	12,000	0.172	0.178	0.185	0.194	0.203
2 (best, start=11000)	8,000	0.114	0.112	0.110	0.109	0.108
	9,000	0.129	0.128	0.128	0.128	0.128
	10,000	0.144	0.145	0.146	0.148	0.150
	11,000	0.160	0.162	0.166	0.170	0.175
	12,000	0.175	0.181	0.187	0.195	0.203
3 (10X pot surv abund)	8,000	0.198	0.194	0.189	0.186	0.185
	9,000	0.225	0.225	0.223	0.224	0.228
	10,000	0.252	0.257	0.262	0.269	0.280
	11,000	0.280	0.292	0.304	0.322	0.346
	12,000	0.309	0.329	0.352	0.384	0.430
4 (0.1X all age comp)	8,000	0.133	0.129	0.128	0.129	0.131
	9,000	0.150	0.149	0.150	0.153	0.157
	10,000	0.168	0.169	0.173	0.179	0.188
	11,000	0.186	0.190	0.198	0.209	0.223
	12,000	0.205	0.212	0.225	0.242	0.264
5 (M=0.17)	8,000	0.127	0.124	0.121	0.118	0.116
	9,000	0.144	0.143	0.141	0.139	0.138
	10,000	0.161	0.162	0.162	0.162	0.163
	11,000	0.178	0.182	0.184	0.187	0.191
	12,000	0.196	0.203	0.209	0.215	0.223
6 (M=0.13)	8,000	0.108	0.106	0.105	0.106	0.106
	9,000	0.122	0.121	0.122	0.124	0.126
	10,000	0.137	0.137	0.140	0.143	0.148
	11,000	0.151	0.154	0.158	0.165	0.172
	12,000	0.166	0.171	0.178	0.188	0.200
7 (M=0.11)	8,000	0.104	0.102	0.102	0.104	0.106
	9,000	0.118	0.117	0.119	0.122	0.125
	10,000	0.132	0.133	0.136	0.141	0.147
	11,000	0.146	0.148	0.154	0.162	0.171
	12,000	0.160	0.165	0.173	0.185	0.199

Table 25. Total F for female sablefish required to obtain yields of 8,000 to 12,000 mt in 1988-1992, assuming constant recruitment (A=1.000).

Run	Yield (mt)	Year				
		1988	1989	1990	1991	1992
1 (best, start=8000)	8,000	0.112	0.110	0.108	0.104	0.101
	9,000	0.127	0.126	0.125	0.122	0.119
	10,000	0.142	0.143	0.143	0.141	0.139
	11,000	0.157	0.160	0.162	0.162	0.161
	12,000	0.172	0.178	0.182	0.185	0.186
2 (best, start=11000)	8,000	0.114	0.111	0.108	0.104	0.100
	9,000	0.129	0.127	0.125	0.122	0.118
	10,000	0.144	0.144	0.144	0.141	0.138
	11,000	0.159	0.162	0.163	0.162	0.160
	12,000	0.175	0.180	0.184	0.185	0.185
3 (10X pot surv abund)	8,000	0.197	0.192	0.182	0.169	0.156
	9,000	0.224	0.223	0.215	0.202	0.189
	10,000	0.252	0.255	0.251	0.241	0.228
	11,000	0.280	0.290	0.292	0.286	0.275
	12,000	0.308	0.327	0.337	0.338	0.333
4 (0.1X all age comp)	8,000	0.132	0.129	0.126	0.123	0.119
	9,000	0.150	0.148	0.147	0.145	0.142
	10,000	0.168	0.168	0.169	0.169	0.168
	11,000	0.186	0.189	0.193	0.197	0.198
	12,000	0.204	0.211	0.219	0.227	0.232
5 (M=0.17)	8,000	0.127	0.124	0.119	0.112	0.105
	9,000	0.143	0.142	0.138	0.132	0.125
	10,000	0.160	0.161	0.158	0.153	0.146
	11,000	0.178	0.181	0.180	0.176	0.170
	12,000	0.195	0.202	0.204	0.202	0.197
6 (M=0.13)	8,000	0.108	0.106	0.104	0.102	0.100
	9,000	0.122	0.121	0.120	0.119	0.118
	10,000	0.136	0.137	0.138	0.138	0.138
	11,000	0.151	0.153	0.156	0.158	0.16
	12,000	0.166	0.170	0.176	0.180	0.184
7 (M=0.11)	8,000	0.104	0.102	0.101	0.101	0.100
	9,000	0.118	0.117	0.117	0.118	0.119
	10,000	0.132	0.132	0.134	0.137	0.139
	11,000	0.146	0.148	0.152	0.157	0.161
	12,000	0.160	0.165	0.171	0.179	0.186

Table 26. Projected yield and total biomass assuming a 1988 harvest of 10,000 mt and 1990-1991 Fs equal to F[MSY]. A Beverton-Holt stock-recruitment relationship was assumed (A=0.889).

Run	B[88]	Y[89]	B[89]	Y[90]	B[90]
1 (best, start=8000)	94,694	9,137	93,324	9,127	92,386
2 (best, start=11000)	95,317	9,021	94,230	9,057	93,635
3 (10X pot surv abund)	62,470	5,688	61,811	6,090	63,351
4 (0.1X all age comp)	78,822	7,825	77,971	7,900	77,840
5 (M=0.17)	87,056	8,720	86,502	8,864	86,695
6 (M=0.13)	99,468	8,800	98,065	8,779	97,094
7 (M=0.11)	102,312	8,352	100,944	8,316	100,056

Table 27. Projected yield and total biomass assuming a 1988 harvest of 10,000 mt and 1990-1991 Fs equal to F[0.1]. Constant recruitment was assumed (A=1.000).

Run	B[88]	Y[89]	B[89]	Y[90]	B[90]
1 (best, start=8000)	94,694	13,061	92,912	12,602	90,430
2 (best, start=11000)	95,317	12,897	93,985	12,519	92,018
3 (10X pot surv abund)	62,471	8,353	62,670	8,749	64,581
4 (0.1X all age comp)	78,822	11,187	78,107	10,930	77,144
5 (M=0.17)	87,056	12,756	86,580	12,513	85,850
6 (M=0.13)	99,467	12,904	97,330	12,407	94,244
7 (M=0.11)	102,311	11,916	100,281	11,502	97,406

Table 28. Alternative scenarios for fishing the west coast sablefish stock down to the B[MSY] level. The harvest in 1988 is assumed to be 10,800 mt.

Year	0.13	0.14	0.15	0.17	0.19	0.23
1989	9000	9700	10400	11600	12900	15400
1990	9000	9600	10200	11300	12300	8200
1991	9000	9500	10000	10900	8200	
1992	8900	9400	9800	8200		
1993	8900	9300	9600			
1994	8800	9200	9500			
1995	8700	9000	8200			
1996	8700	9000				
1997	8600	8900				
1998	8600	8200				
1999	8500					
2000	8500					
2001	8500					
2002	8400					
2003	8400					
2004	8400					
2005	8400					
2006	8300					
2007	8300					
2008	8200					

Conclusion

The most likely scenario for sablefish is described by run #1 which strikes a compromise between the decline in the pot index and the relatively high frequency of old fish in the 1987 fishery samples. The mean total biomass during 1988 was 94,700 mt and the age 3+ biomass was 78,600 mt. The biomass levels at the beginning of the year were 107,500 and 89,600 mt, respectively. The total F imposed by a 10,000 mt fishery will be 0.14. We projected future abundance levels using both constant recruitment and Beverton-Holt stock-recruitment functions. Although we do not yet have evidence of declining recruitment at lower spawner biomass levels, we note that the spawning biomass at MSY is only about 25% of the virgin spawning biomass. This large reduction in spawning biomass probably occurs because the fish are available to the trawl fishery several years before they mature. A prudent course of action is to utilize the Beverton-Holt recruitment function to estimate potential yield from the stock. If a 52:48 trawl:fixed gear allocation is maintained, then the MSY for this stock is 8,200 mt at a mean age 3+ biomass of 67,800 mt. An ABC of 9,100 mt is indicated by applying the F[MSY] to the current stock structure. At this level of fishing mortality, and if there are no great deviations in recruitment, the stock would be near the biomass yielding MSY in about 20 years and the ABC would be reduced to 8,200 mt. Our current assessment does not account for trawl discards occurring after the end of the season or additional discarding caused by restrictive trip limits. Subsequent analyses will account for these factors, but we note here that total fishery-induced mortality will be greater than the 9,100 mt ABC, so the stock is being fished down to the B[MSY] level more rapidly than predicted above.

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Appendix Table 1. Age composition data.

```
Data template is:
year type  sex  N aged
  age1      2     3     4     5     6     7     8     9    10
    11     12    13    14 15-19   20+

 83   5    1    216.
   1.1     14    51    57    28    26    10   6.8   4.8   9.5
   2.5    1.9     0     0   2.7   1.1
 83   5    2    326.
   0.4     29    32   115    40    51    24   8.4   7.6   0.8
   5.1      5   1.4     2   3.9   0.7
 85   5    1    661.
   0.7     40   101   137   148   107    68    29    15   4.2
   7.4    2.4   1.1   1.3     0     0
 85   5    2    553.
     1     75   113   111    85    86    34    20   8.7   6.5
   4.3    2.3   3.4   1.4   0.7   1.0
 86   1    1    119.
   0.8    2.4   4.6   7.8  11.7  11.8  11.1   7.8   8.5   6.9
   6.2    3.2   3.4   4.0   8.7   1.1
 86   1    2    224.
   0.6    5.5   6.0   8.8  14.5  14.0  12.4   8.4   6.3   5.0
   4.2    2.7   2.3   2.9   3.7   2.8
 86   2    1    636.
   2.5    8.4   8.8  12.7  13.1  11.2   9.2   6.0   6.1   5.2
   4.0    1.8   2.1   2.4   5.4   1.0
 86   2    2    642.
   7.0   16.6  12.0  11.2  14.3  11.5   7.7   5.1   2.7   2.7
   2.0    1.2   1.3   1.4   1.6   1.7
 87   1    1    189.
   0.0    2.5   3.5   3.9   4.0   4.6   9.0   7.6   4.9  10.9
   2.9    4.0   3.6   3.1  13.1  22.4
 87   1    2    216.
   0.1    2.5   4.8   5.4   7.7   5.5   8.5   9.7   8.5  13.1
   2.8    3.4   2.8   2.0  10.6  12.7
 87   2    1    604.
   1.4   16.2  10.5   7.3   6.6   5.2   7.7   5.7   4.4   7.3
   2.4    2.5   2.4   1.5   6.9  12.1
 87   2    2    702.
   2.3   22.0  18.3  11.3   8.7   5.8   5.2   4.2   4.1   5.0
   1.3    1.5   1.4   0.6   3.4   4.9
```

Appendix Table 2. Size composition data where size is measured in cm fork length.

```
Data template is:
year type sex  Nmeasured
 32-35 36-37 38-39 40-41 42-43 44-45 46-47 48-49 50-51 52-53
 54-55 56-57 58-59 60-63 64-67 68-71 72-75 76-79 80-90  90-

  71   5   1    690.
   0.0   0.0   0.0   0.0   1.3  18.5  39.2  75.1 108.0  85.8
  70.6  86.5  65.8  71.6  46.4  14.7   4.0   1.9   0.9   0.0
  71   5   2   1227.
   0.0   0.0   0.0   0.0   1.3   3.4  23.7  58.6  77.8 120.0
 101.0  91.9  58.3 144.0 155.0 132.0 115.0  80.2  63.6   1.3
  79   5   1   1138.
   0.0   0.0   0.0   0.0   4.9  52.6 159.5 301.8 444.1 584.8
 584.1 409.8 250.8 245.7  48.6   7.3   4.0   0.0   0.0   0.0
  79   5   2   1079.
   0.0   0.0   0.0   2.0   6.1  36.4  76.5 135.2 180.9 235.2
 257.9 243.2 256.2 411.3 327.4 290.7 145.0  88.0  54.0  15.0
  80   4   1    338.
 108.7 243.7 286.1 147.3  51.7  37.4  97.7  85.1  46.1  24.6
   6.3   4.2   0.9   1.3   0.1   0.9   0.6   0.0   0.0   0.0
  80   4   2    328.
  42.6 171.1 261.2 145.6  46.2  27.1  71.3 129.4  76.0  42.6
  13.5   8.3   2.4   4.2   0.2   0.3   0.6   0.9   0.6   0.0
  80   5   1   1050.
   0.0   0.0   1.0   0.0  14.4  85.5 245.9 437.0 503.2 452.8
 376.8 256.1 161.3 197.8  67.5   8.3   2.5   0.0   0.0   0.0
  80   5   2    888.
   0.0   0.0   0.0   7.0   3.6  29.5 129.1 227.0 305.8 317.2
 283.2 169.9 147.7 219.2 170.5 138.7 107.5  76.0  41.0   6.0
  81   5   1    755.
   0.0   0.0   0.0   1.0   9.0  43.3 156.9 312.9 365.9 346.7
 219.0 144.1  72.4  93.3  38.4  11.2   0.0   0.0   0.0   0.0
  81   5   2    655.
   0.0   0.0   0.0   0.0   0.0   6.7  48.1  94.1 176.1 227.3
 219.0 141.9 142.6 144.7 117.6  75.8  75.0  41.0  27.0   0.0
  83   4   1   1584.
 304.1 516.0 423.8 248.9 413.1 354.5 226.6 171.5 108.4  57.1
  54.6  17.5  18.8  13.7  10.2   7.5    .5   0.0   0.0   0.0
  83   4   2   1784.
 195.9 451.2 286.7 218.3 335.6 428.2 325.6 234.3 165.2 135.2
  60.1  45.4  39.6  38.3  12.6   5.6   4.9   3.0   1.3   0.0
  83   5   1    250.
   0.0   0.0   2.0  12.0  35.2  79.8 180.3 283.5 337.0 209.6
 175.6  81.2  54.2  46.4   6.6   0.0   0.0   6.5   0.0   0.0
  83   5   2    350.
   0.0   0.0   2.0   0.0  11.7  53.2 109.7 148.5 158.0 255.4
 226.4 209.8 141.8 192.6 112.4  74.0  44.0   6.5  14.0   0.0
  84   6   1    609.
   0.0   0.0   1.0   0.0  76.0 205.8 536.9 823.2 903.4 700.5
 429.5 292.9 131.8 125.5  32.1   0.0   0.0   0.0   0.0   0.0
  84   6   2    749.
  0.0   0.0   0.0  16.0  19.0 112.2 185.1 285.8 427.6 456.5
499.5 360.1 355.2 454.5 246.9  97.0  48.0  24.0  16.0   0.0
 85    5    1     661.
  0.0   1.0   2.0  18.0  64.0 209.4 408.3 582.2 534.7 381.1
238.4 162.2 121.5 118.7  33.7  17.6   6.0   1.5   0.0   0.0
 85    5    2     553.
  0.0   1.0   2.0  12.0  64.0 160.6 237.7 231.8 260.3 265.9
175.6 155.8 124.5 183.3 101.2  75.4  42.0  14.5  15.0   1.0
 86    1    1     475.
  0.0   0.0   0.0   1.1   0.2   0.6   4.3   5.6  12.0  18.1
 13.0  11.1  12.7  11.6   6.9   2.3   0.1   0.0   0.4   0.0
 86    1    2     832.
  0.0   0.0   0.0   0.3   0.5   1.3   4.0   3.3   7.7  10.8
 10.4   8.7   9.4  13.6  12.2   7.9   5.0   2.0   2.6   0.3
 86    2    1    2202.
  0.0   0.0   0.0   2.2   2.9   6.7   8.0  13.9  16.1  14.6
 13.5   9.2   5.2   5.1   1.9   0.8   0.1   0.0   0.0   0.0
 86    2    2    2366.
  0.0   0.0   0.0   5.7   4.2   5.8   9.3  11.8  12.9   9.8
  9.6   8.3   5.9   9.5   3.4   2.0   0.8   0.4   0.6   0.2
 86    4    1    2442.
355.1 604.7 521.2 289.1 153.5 109.5 107.6  70.1  28.4  22.5
 21.9  15.8  16.0  40.0   7.7   4.6   2.9   0.0   0.0   0.0
 86    4    2    2274.
235.8 482.2 499.9 323.0 134.5 114.0  87.0  85.9  70.6  55.1
 29.6  20.2  28.0  77.9  53.9  79.9 102.2  80.2  39.3   9.7
 86    6    1     417.
  0.0   0.0  13.0   0.0  72.3 117.7 217.7 317.3 326.3 320.9
254.3 118.4  84.4  30.3  11.5  10.0   0.0   0.0   0.0   0.0
 86    6    2     468.
  0.0   0.0   0.0  37.0  20.7  39.2  94.3 172.7 210.7 171.1
193.7 210.6 183.6 299.7 191.5  70.0  32.0  15.0  18.0   0.0
 87    1    1    1130.
  0.0   0.0   0.0   0.0   0.7   2.2   3.4   5.3   8.0  13.6
 19.5  16.7  11.8  11.6   4.6   2.6   0.1   0.0   0.0   0.0
 87    1    2     987.
  0.0   0.0   0.0   0.3   0.1   1.0   1.9   2.1   2.6   7.3
  9.3  10.9   9.5  17.7  15.5  10.1   7.5   2.0   1.8   0.3
 87    2    1    2479.
  0.0   0.0   0.0   5.9   8.1  10.9  10.5  10.6  11.9  12.7
 11.7   7.5   4.4   4.6   0.6   0.2   0.2   0.0   0.0   0.0
 87    2    2    2222.
  0.0   0.0   0.0   7.7   6.6   9.7  11.8  10.3  10.5   9.6
 10.0   6.4   6.0   5.5   2.9   1.4   1.0   0.4   0.3   0.1
 87    5    1     444.
  0.0   2.0   3.0  13.3  14.4  56.6 133.4 265.7 269.2 235.8
188.8  81.3  39.2  55.2  18.9   8.2   0.0   0.0   0.0   0.0
 87    5    2     302.
  0.0   0.0   6.0   1.7  11.6  15.4  39.6  96.3  80.8 105.2
 90.2  92.6  62.8  84.8  67.1  40.8  19.0   7.0   7.0   1.0
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The Biological Mechanisms of Tooth Eruption and Root Resorption,
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Is tissue resorption and replacement in permanent teeth of mammals caused by stress-induced hypocalcemia?

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Summary

Natural resorption and repair of tissues in permanent teeth of mammals are often attributed to restricted odontoclastic and cementoclastic activity under localized control. I suggest that in addition to the well known local causes, systemic alteration of dental tissues caused by regulation of blood-serum calcium is common also. This newly recognized type of tissue alteration apparently affects teeth internally and externally, and interferes with normal rates of tissue calcification as well. Causal connections between systemic alteration in tooth tissues and stress-induced low serum calcium (hypocalcemia) in mammals are indicated by this study but are not directly demonstrated. Two theoretical models are presented that explain how certain manifestations of stress may produce different responses and results.

Introduction

Localized dental resorption and repair

Many dental scientists view resorption and repair of tissue in permanent teeth as having strictly proximate causes. It is thought that odontoclastic or cementoclastic activity occurs in response to local injury, pressure, disease or malocclusion. Most alteration occurs in external cementum of root bases of single teeth or a few adjacent teeth, although penetration into dentine is not unusual. More importantly, this type of tissue alteration is reportedly not directly influenced by systemic episodes or events. This has led many workers to conclude that in most cases, permanent teeth probably cannot respond to systemic control and that there are no other important factors responsible for resorption and repair of tooth tissues beyond those of exclusively local origin (Fish 1932; Kronfeld 1949; Ferguson and Hartles 1964; Scott and Symons 1964; Jenkins 1966; Jones and Boyde 1971; Rasmussen 1972; Eanes and Termine 1983; Veis and Sabsay 1983).

Systemic dental resorption and repair

There are many reasons for thinking that, although locally induced alteration may be common, it may not be the only major mechanism. Our knowledge of calcium kinetics is already adequate to construct a fairly convincing *prima facie* case for systemic resorption and repair in teeth, and the evidence seems at least plausible, even if the resorption has not been reported before.

1. Calcium is critically important to virtually all of a mammal's physiological processes (Martin 1985; Miller 1987). 2. Teeth are a rich calcium source, with the same percentages of calcium phosphate as bone (Eannes and Termine 1983). 3. Presumably, teeth are affected by the same cells, hormones (Boyde, Ali and Jones 1984, 1985; Thoma 1954; Sullivan and Jolly 1957; Scott and Symons 1964), and processes that build and destroy bone tissue (Symonds *et al.* 1966; Braithwaite, Glascock and Riazuddin 1969; Parfitt 1976). 4. In addition, dental formative surfaces are attended by and exposed to the same circulatory system that delivers calciostatic hormones to bone (Saunders and Röckert 1967).

In mammals, under at least several stressful conditions, including giving birth (parturition), blood serum calcium may temporarily fall below the normal range. Low serum calcium (hypocalcemia) occurs because calcium intake into the blood is exceeded by calcium loss from circulation. Restoration of serum calcium to normal levels is usually brought about when calcium is borrowed from the body's solid, semifluid and fluid calcium compartments, such as bone and extracellular tissues. The resulting calcium debt in non-serum calcium compartments is due to actions of serum parathyroid hormone (PTH) on bone cells and on

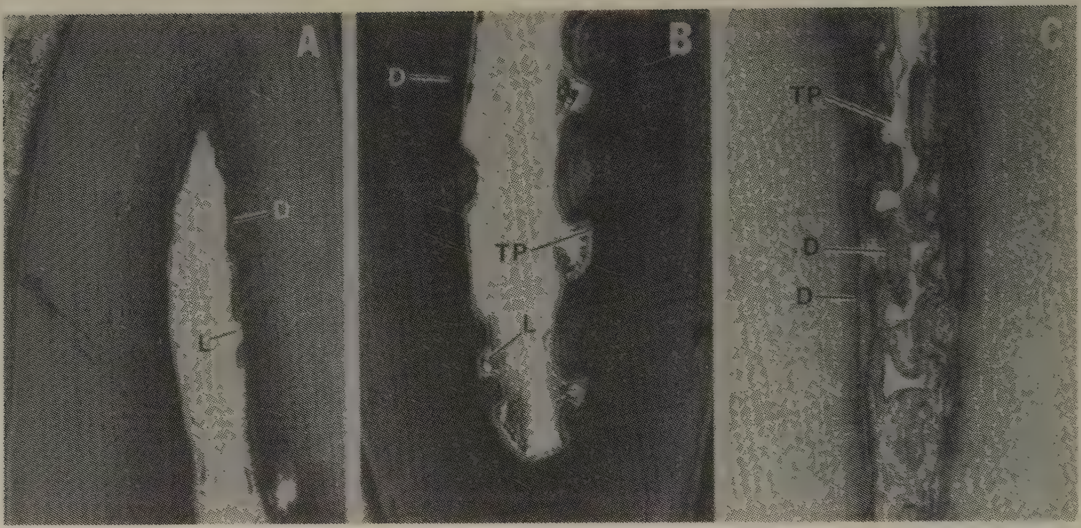

Fig. 1 Progressive stages of mineralization interference in dentine along pulpal margin in dolphin teeth. A. Incipient stage of local interference (L) on right side and regional interference on left side. Usually dark layer (D) of dentine appears to define a break in the regular layering pattern. B. Intermediate stage showing scalloped development typical of localized interference and thickened predentine (TP) within scallops. C. Advanced stage of interference showing convoluted scallops with noticeably thickened predentine.

ionic enzyme pumps that transfer calcium across compartmental membranes to blood (Braithwaite *et al.* 1969; Parfitt 1976; Gorbman *et al.* 1983). The calcium debt is usually repaid after conditions normalize, but during hypocalcemic conditions every accessible calcium source, including teeth, should be affected.

This report has three major objectives. The first is to describe a previously unrecognized mechanism for dental-tissue alteration in mammals that apparently responds to systemic calcium regulation. The second is to consider the yet unproven likelihood that stressors, changes in serum calcium and tooth-tissue alteration are causally related. The third objective is to illustrate some effects of stress on serum calcium by proposing two theoretical models involving cases of hypocalcemia, in this study and in reports by others.

Methods and materials

Dental-tissue-alteration samples

The present study came about serendipitously. I first recognized resorption and reparation features in decalcified and stained thin sections of dolphin teeth during age estimation studies (Myrick *et al.* 1983). Initial examination of a few hundred teeth indicated the need for a thorough study of dental tissue alteration in dolphins. I concluded the study on dolphins after having microscopically examined teeth from more than 2500 individuals.

The samples included teeth from spinner *(Stenella longirostris)*, spotted *(Stenella attenuata)* and common *(Delphinus delphis)* dolphins, killed in an eastern Pacific commercial purse-seine fishery in which dolphins are chased and netted to catch the yellowfin tuna that follow the dolphin schools (Perrin 1969; Perrin, Coe and Zweifel 1976). The samples also included teeth from bottlenose dolphins *(Tursiops truncatus)*, which are not affected by a fishery; these were collected primarily from carcasses beached along the coasts of California and Baja California.

Each sample contained specimens of all ages and both sexes, except common dolphins of which only males were available. In about 300 of the more than 2500 specimens, from two to six teeth of single individuals had been prepared. These permitted me to compare features in two or more teeth from the same animal in slightly more than 10% of the specimens examined.

In addition, to determine whether similar dental-tissue alteration occurred in other mammals, I examined thin sections of teeth from 9 Montana black bears *(Ursus americanus)*, 10 Rocky Mountain elk *(Cervus elaphus)* and 1 bobcat *(Felis rufus)* from New Mexico. I also studied photographs of teeth from other mammals, including humans.

Results

Dolphin teeth

The dolphin teeth showed the effects of alteration in various stages, in various combinations, with and without repair and with and without evidence of repetition of resorption and repair. I recognized three basic forms of alteration. Each form showed one or more types of physical expression (types). All three forms apparently originated at the for-

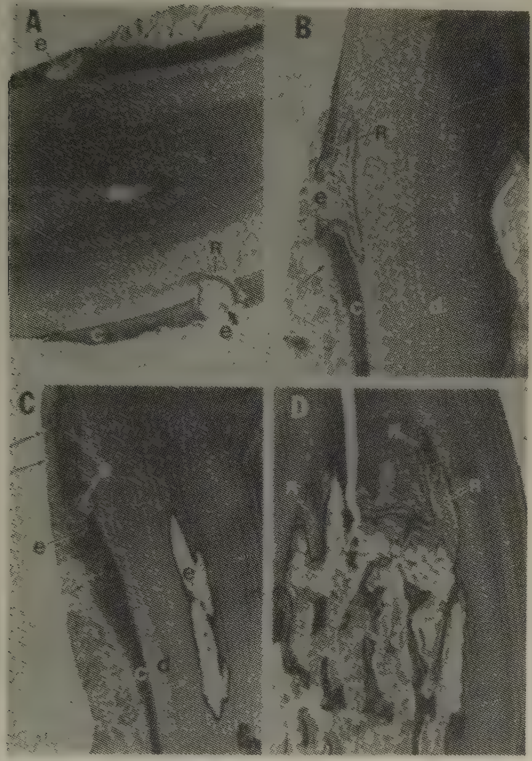

Fig. 2 Stages of excavational resorption in cementum (c) and dentine (d) of dolphin teeth. A. Earlier resorption of tooth is marked by partially repaired (R) excavations (e) on each border. Arrows indicate possibly new resorption activity. B. Example of more extensive excavational resorption which has been lined with reparative material (R). Arrows indicate possible second cycle of resorption. C. Advanced stage with arrested activity within cementum (e) and apparently active unrepaired areas in dentine (e). Arrows show areas of possible impending second cycle of cemental resorption. D. Severe resorption features indicating, by crosscutting lines, activity has been repeated. Fibrous tissue fills lower portion of resorption cavity. (R indicates areas repaired by bone- or cementum-like materials.)

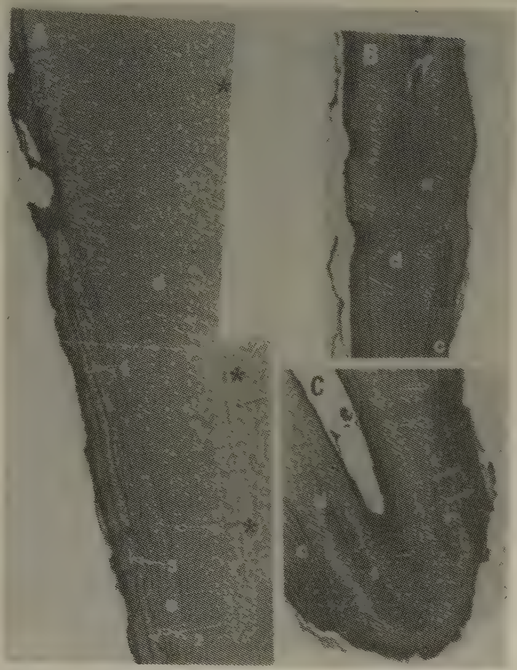

Fig. 3 Resorption in dental tissues of black bears. A. Numbered arrows indicate series of resorption episodes in cementum. Number 1 indicates areal resorption with repair that crosscuts the dentinal (d) layers. Other numbers indicate combinations of areal and excavational resorption with repair. Asterisks indicate possible local mineralization interference along dark line that may represent regional interference. B. Opposite side of tooth shown in 3A. Wide, irregular reversal line caused by areal resorption apparently done in second winter with repair (R) completed before third winter. C. View of tooth of bear older than that represented by 3A and B. Cycle-like minor areal resorption (arrows) in cementum (c) with repair indicating activity was concurrent with dark layer formation.

mative surfaces of dentine (along the pulpal margin) and cementum (along the external surface of the root).

1. Mineralization interference (develops continuously). This was so-named because the affected tissues appeared either never to have been properly mineralized or because mineralization was delayed while the protein matrix continued to form.

Interference was recognizable by some abrupt change in the pattern of layers (Fig. 1), usually a strong discontinuity in pattern or a layer that was especially dark, followed by a gap in layering (similarly stained layers were interpreted by Klevezal and Myrick [1984] as indicating parturition in mature female dolphins). The layering hiatus was followed in turn by a noticeably thickened unmineralized predentine or precementum.

This form of alteration was of two types: 1) regional, which occurred along extensive portions of a formative surface, and 2) local, which occurred at regularly spaced sites along a formative surface. Regional interference in cementum often showed unusually thin mineralized cemental tissue. Local interference was identifiable by wavy (early stage) to scalloped (advanced stage) tissue margins with layers usually evenly spaced in the convex portion and squeezed together (but not truncated) in the concave portion (Figs. 1B and C). Neither of the two types of mineralization interference showed repair. Because of the absence of replacement materials and because the alteration evidence was parallel to the formative surfaces, regional interference was the most difficult to detect. Presumably many cases of this type of alteration escaped my notice.

2. Areal Resorption (develops continuously). Areal resorption showed massive removal of tissue sub-parallel to the layering plane, such that resorptive edges (or reversal lines) cut incongruently as a wide front across layers next to resorption areas (Fig. 3). Areal resorption was not ac-

companied by thickened predentine or precementum. Additionally, in some specimens partial repair of resorbed areas by cementum- or bone-like material occurred.

3. Excavational Resportion (known also as "dissection resorption" or "tunneling resorption" when found in bone [Grech *et al.* 1985]). This form of alteration was easily defined because it occurred in many stages of development. Reversal lines were almost always without any particular orientation. I recognized nine stages from incipient to advanced, which I define below:

Stages

A. formative margins with slight depressions which tend to truncate tissue layers;
B. depressions deepened, becoming pit-like;
C. pits tend to be elongated, forming short tunnels;
D. C stage with replacement bony tissue;
E. long tunnels, directed inwardly toward dentine if originated from cementum, but coincide with orientation layers if from dentine;
F. E stage with replacement bone or other repair tissue;
G. expanded and elongated tunnels, usually penetrating dentine if from cementum, tending to obliterate large areas of dentine and pulpal margin if internal in origin;
H. G stage with replacement bone or other tissue;
I. G, H and earlier stages with crosscutting tissues indicative of separate, repeated alteration reactions.

Of the stages of excavational resorption, I regarded C through E as intermediate, and F through I as advanced (Figs. 2A-D).

Replacement of resorbed areas in dolphin teeth usually was with cementum-like or bone-like materials. Reparation with dentine was never observed. In most of the specimens that had undergone replacement activity, the repair materials usually only lined or partially filled (i.e., they rarely were completely filled) the resorbed region (Figs. 2B-D). To a noticeable extent reparation materials included fibrotic tissue (Fig. 2D) similar to that described in cases of human idiopathic resorption of teeth (Thoma 1954; Goldman 1954; Sullivan and Jolly 1957).

Nearly all specimens in the dolphin-tooth samples revealed at least incipient stages of one or more alteration forms. In approximately 90% of the more than 300 specimens in which more than one tooth was available from an individual, each of its teeth showed the same alteration form(s) and at least similar stages of alteration.

To estimate the extent of some of the different forms of alteration among the samples, I made some preliminary counts, by sex and species, of several forms and stages of alteration (Table 1). To test for significance of results, I used variance tests for homogeneity in proportions (Snedecor and Cochran 1973). A tally of male and female spinner dolphins significantly showed that the presence of regional mineralization interference in cementum was detected in females more than twice as often as in males (64% vs. 28%). Female spinner dolphins showed almost no (1%) detectable sign of regional and local mineralization interference in dentine whereas 28% of female spotted dolphins exhibited both types of interference alteration; this difference was significant. Of the four dolphin species, my counts of specimens showing intermediate or advanced excavational resorption for cementum indicated a significantly higher incidence in spinner dolphins than any other species. For excavational resorption, female spinner dolphins showed nearly twice the detectable frequency as male spinner dolphins. Bottlenose dolphins, the one sample not collected in the purse-seine fishery, had the lowest incidence of this alteration form. However, two other species samples that were from the fishery (common dolphin males and spotted dolphin males and females) did not have significantly higher percentages than the bottlenose dolphins for this form. These preliminary comparisons indicated that activity in such alteration forms differed by species and sex, and at least for cementum of spinner dolphins, females showed substantially more alteration than males.

Table 1. Sex and species differences in degree and frequency of some types of dental tissue alteration in mature dolphins.

Species	Sex	Number in Sub-sample	Tissue and Alteration Form			
			CEMENTUM: Regional Mineralization Interference			
			%	(N)		
1. *S.longirostris*	female	*200	64	(128)		
2. *S.longirostris*	male	150	28	(42)		
			DENTINE: Regional and Local Mineralization Interference			
			%	(N)		
1. *S.longirostris*	female	*420	1	(4)		
2. *S.attenuata*	female	*316	28	(90)		
			CEMENTUM: Excavational Resorption			
			Intermediate and Advanced		Advanced Only	
			%	(N)	%	(N)
1. *S.longirostris*	female	782	30	(235)	15	(112)
2. *S.longirostris*	male	710	17	(120)	8	(57)
3. *D.delphis*	male	59	3	(2)	3	(2)
4. *T.truncatus*	male & female	141	1	(2)	1	(1)
5. *S.attenuata*	male & female	*335	3	(10)	1	(5)

*Indicates that some of the same specimens of a subsample were used to evaluate two or more types of alteration.

Human teeth: idiopathic resorption

Dolphin teeth showing intermediate and advanced stages of excavational resorption were identical in almost every detail to photographs of human teeth depicting "idiopathic resorption" (hereafter referred to as I.R.) (Sullivan and Jolly 1957; Stanley 1965). Published photographs and descriptions indicated that I.R. invasion starts either from within the pulp cavity, so-called "internal resorption," or along the outside surface of the root, "external resorption" (Thoma 1954; Stanley 1965; Fullmer 1984). Both patterns of invasion were in dolphin-tooth samples also. As in excavational resorption seen in dolphins, most tunneling in I.R. examples is without specific orientation.

Because I could detect no important differences between dolphin excavational resorption and human I.R., I suggest that they were derived by similar processes. In advanced I.R., large amounts of original tissue were absent and pulpal margins were obliterated. Repeated crosscutting of resorption and repair structures (Sullivan and Jolly 1957; Stanley 1965) was similar to that in advanced stages of excavational resorption in the dolphin teeth. Like much of the reparation in the dolphin teeth, I.R. cases (Thoma 1954; Stanley 1965) indicate that repair material is of bony, cemental and fibrotic tissue, which often incompletely fills the resorption cavities.

Teeth of other mammals

Seven black bear specimens, the bobcat specimen and all ten elk teeth showed features of dental-tissue alteration. Photographs of teeth of racoons, a badger, river otters, coyotes, domestic sheep, mule deer and moose (provided at random by G. Matson) revealed alteration and repair features as well.

Black bears

Dentine of most black bear specimens showed only a few thin layers with some waviness, which I interpreted as minor regional and localized mineralization interference. However, all three forms of alteration in cementum, resembling those in dolphin specimens, occurred in several bear specimens. Especially obvious were repeated excavational resorption features alternating with repair materials and areal resorption structures.

The tooth of a five-year-old bear showed three forms of alteration in cementum and two in dentine (Fig. 3). The cementum contained a succession of reversal lines that delimited repeated local excavational resorption of tissue formed earlier. Peripheral to the sites of resorption, each reversal line was continuous with a corresponding thin, straight, dark-stained, cemental layer that marks the end of a year's deposition, i.e., formed just before hibernation (Stoneberg and Jonkel 1966). This indicated to me that resorption activity began during or shortly after deposition of a dark layer. Based on the sequence of crosscutting reversal lines, at least four such resorption periods must have occurred in this animal's lifetime, each separated by about a year (i.e., an annual layer) (Figs. 3A and B). The most severe response apparently was in the second annual resorption period, interpreted from cemental layers as the second winter of life. This was indicated by extensive areal resorption along a broad front that transgressed the dentine at an angle to its layers on both sides of the tooth. Despite the presumed severity of the resorption, complete repair was accomplished by the early part of the following year, well before the formation of the third dark layer.

Thus, most detectable alteration in the black-bear sample occurred in winter and was usually fully repaired before the following winter. Several specimens showed it to have occurred on a regular basis (i.e., every year or so).

Elk

The elk specimens revealed a variety of alteration features, although repeated cemental excavational resorption and local mineralization interference in the dentine occurred in all specimens. As in black bears, dark-stained winter cemental layers in the elk specimens (Keiss 1969) were associated with irregular reversal lines of excavational resorption showing usually (but not always) complete cycle-like repair. In some specimens, replacement materials of excavational resorption included fibrotic tissue, which resembled the advanced stages in human I.R. and dolphin excavational resorption. Scalloping of the pulpal margins as a result of local mineralization interference was in an advanced stage in the dentine of some of the elk. However, the scalloping was not as regularly spaced and had thinner marginal predentine than advanced examples in dolphins.

Thus for elk, detectable alteration activity occurred during the formation of the winter layer. Repeated patterns of such structural associations indicated that alteration tended to occur with regularity. Advanced stages of resorption and interference and occasionally incomplete repair, sometimes with fibrotic tissues, suggested severe responses with little recovery.

Bobcat

After a 30-pound male bobcat was killed in a trap near White Sands, New Mexico, on 28 January, 1986, one of its teeth was prepared for age determination. Its layered cementum indicated an age of about six years. A reversal line occurred in the cementum after the fifth dark annual layer had been deposited (i.e., in winter 1984-85). The reversal line showed excavational resorption through all previously formed cemental tissue, penetrating almost into the dentine. Before the bobcat died, a sixth dark layer had formed over an extensive resorption area that was incompletely repaired (Fig. 4).

After examining the bobcat specimen, I studied recent historical climatological data of the trap area. The data suggested possible connections between resorption and abnormally severe climate before and during the presumed time of resorption. Conditions were quite dry locally in 1983, with a winter (1983-84) of prolonged cold. Precipitation was only somewhat more than normal (14.88" vs. 12.35") in 1984-85 but all of it fell as snow. (The winter of

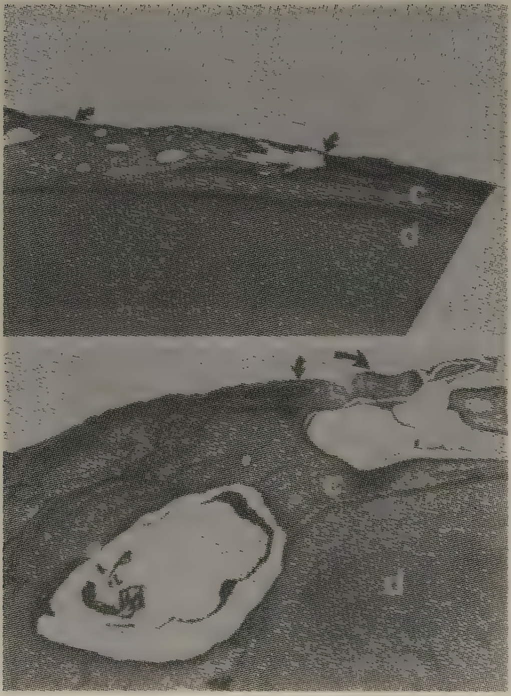

Fig. 4 Unrepaired cemental excavation in tooth of six-year-old bobcat (d = dentine, c = cementum). Five dark layers are truncated and damage is partially roofed over by a sixth dark layer (arrows). This is interpreted as resorption that occurred during the animal's fifth winter, which was relatively severe. Possibly, lingering ill health prevented repair of resorption damage.

1984-85 had a period of extreme cold with almost 15 inches of snow compared to a normal annual snowfall of zero inches.)

Thus, based on the position of the reversal line, resorption occurred after a year of abnormally cold temperatures and during the 1984-85 winter of record high snowfall. The evidence in this example was not strong; the bobcat's physical condition was unknown and its geographical position during the severe climate was only presumed to be near the trap site.

Discussion

Systemic control of tissue alteration

The study of the samples yielded strong evidence that the features of dental-tissue alteration observed were products of systemic—not local—control. Several of the most important points follow:

In the dolphin samples, when more than one tooth (up to six teeth) was available from an individual, each tooth usually showed the same forms and stages of alteration. Such a situation should be rare in localized alteration. In jaw samples from which dolphin teeth showing alteration had been removed, there were no signs of tumor, infection, or mechanical injury; such signs should be obvious in many cases of localized alteration. Usually the sites of resorption were not near root bases. Root-base resorption is common in locally induced resorption. In some dolphin species, features of alteration originating from within the pulp cavity were frequent, whereas local resorption usually originates externally. Frequency data indicated that females tended to have detectable alteration features twice as often as males of the same species; this could not be easily explained by localized control. Excavational resorption and fibrotic repair of dolphin teeth are evidence for hyperparathyroidism when it occurs in bone (Gaillard 1959; Rasmussen 1961; McLean and Urist 1968; Raisz 1976; Martin 1985; Grech *et al.* 1985). Repeated alteration and replacement were indicated within the same resorption site. Repetitious internal resorption and repair at the same site would be difficult to explain without invoking systemic processes.

In the cases of I.R. in human teeth (which I studied from descriptions and photographs in other reports), those features in dolphin teeth characteristic of hyperparathyroidism in bone, including dissection resorption (Gretch *et al.* 1985) and fibrotic replacement materials, occurred also in human teeth with I.R. (Thoma 1954; Goldman 1954; Sullivan and Jolly 1957). When I.R. is discovered, several teeth from adjacent or diverse positions are found, with some frequency, to be affected once or repeatedly over a short period in the same individual (Thoma 1954; Stanley 1965). The presence of damage in several teeth in otherwise apparently healthy humans is evidence for non-localized resorption factors. The unknown cause or causes of I.R. (Mummery 1920; Sullivan and Jolly 1957; Fullmer 1984) was taken as additional evidence of non-localized alteration. Symptoms have not been sufficiently consistent to identify ultimate cause because most cases have been discovered after the condition has reached advanced stages and caused pain (Sullivan and Jolly 1957; Stanley 1965). Patients in these cases reported no local pressure and experienced no local tumor, injury, infection or malocclusion, while the I.R. condition developed into advanced stages identical to those in excavational resorption seen in dolphin teeth.

Evidence from the bobcat study is weak because data were lacking concerning the bobcat's condition and whether the animal was a long-standing resident of the area in which it was trapped. Nevertheless, circumstantial evidence supports a (systemic) connection between cemental alteration and environmental conditions. The otherwise neatly layered cementum was presumably excavated suddenly in 1984-85, at about the time of the unusually harsh weather in the area.

Evidence was clear that dental alteration in the black bears and elk was under systemic control. Alteration features were repeatedly connected to winter periods. Of striking importance was that activity resulting in complete replacement almost always occurred between winter resorption bouts. Cyclic control of such well-timed alteration in so many individuals could be most easily explained by systemic controlling factors.

Implications of systemic control

In this report I have marshaled evidence that a previously unrecognized type of dental-tissue alteration may commonly affect distantly related mammals and that this alteration is under systemic control. If this is correct, then the proximate controller is serum calcium, just as it is in bone-calcium turnover.

Under hypocalcemia, calcium-borrowing is initiated by actions of increased serum PTH. I presume that when calcium is borrowed from tissues or fluids near the teeth, tooth tissues would be resorbed by activity of clastic cells, or mineralization interference would occur as calcium ions are drawn away from mineralization sites. In normocalcemia, PTH activity is suppressed, calcium is deposited at normal rates and any calcium debt accrued by the tissues may be repaid. In teeth, this should initiate repair activity.

It seems likely that the longer calcium-borrowing occurs, the more time and calcium are required to complete repair or repayment after stabilized normocalcemia suppresses PTH. If normocalcemia is only intermittent, interspersed for short periods by repeated periods of hypocalcemia, PTH release would increase intermittently and calcium deposition would tend to be inhibited. Repair of dental tissues would not occur at all or would occur only sporadically and incompletely, perhaps with non-calcified tissues such as fibrotic tissue (as in the dolphin specimens). Intermittent hypocalcemia (and hyperparathyroidism) might also result in repeating (crosscutting) structures of resorption and repair, as I have described in dolphins, bears, elk, and which has been reported in humans.

Conversely, if periods of normocalcemia are sufficiently long, tissue should become fully repaired (as in the bears and most of the elk specimens). However, crosscutting resorption structures with repeated incomplete repair (as in human I.R. cases and dolphin specimens) should indicate that periods of normocalcemia were too short or interrupted too often by periods of hypocalcemia.

Thus, one may begin to infer, by reversing the terms in the argument, that members of a mammal population are likely to be chronically hypocalcemic if the occurrence of poorly repaired systemic resorption damage is found to be common. Further, hypocalcemia of population members would be expected to be seasonal or to occur in some sort of cycle if fully repaired and repeated damage from systemic resorption is found to be common.

Causes and symptoms of hypocalcemia

In most mammals the serum calcium value usually falls within a narrow range of 9.0 to 11.0 mg/100 ml (Berkow 1982; Martin 1985; Porat and Sherwood 1986). A mammal is hypocalcemic when its serum calcium falls to levels below about 9.0 mg/100 ml. If serum calcium continues to fall to 7.0 mg/100 ml or less, hypocalcemia is regarded as already severe and PTH secretion is quickly elevated to its highest rate and calcium recruitment activity is maximized (Gorbman *et al.* 1983).

One result of hypocalcemia is resorption of dental-tissue and presumably even greater bone resorption. In severe hypocalcemia or at least in more severe responses, symptoms of tetany begin to occur in many mammals. Susceptible animals show depression, dullness, ataxia and neuromuscular hyperexcitability. These signs may be followed by twitching, convulsion, regional paralysis and death.

How is it then that PTH actions do not normalize serum calcium before symptoms of tetany progress or before extensive resorption occurs?

There is no general agreement as to major causes of hypocalcemia in apparently healthy mammals. However, there is growing recognition among endocrinologists that in healthy, susceptible mammals low serum calcium results from responses to stress stimuli of various sorts, including temperature extremes, exhaustive exercise, starvation, injury and fear (Martin 1985; Gorbman *et al.* 1983; Viru 1985). Noxious stimuli are received via the hypothalamic-pituitary-adrenal pathway. Stimuli of sufficient strength, duration, or frequency evoke hypersecretion of glucocorticoids (principally cortisol). Depending on the stressor, cortisol is released into the blood in concentrations of up to 10 times normal amounts (Gorbman *et al.* 1983; Martin 1985), and secretion and release can continue or recur for days or weeks (Martin 1985; Viru 1985).

The elevation of serum steroids reportedly decreases serum calcium in at least two ways: 1. it increases excretion of calcium by the kidneys and so net calcium loss is accelerated, and 2. it transfers ionic calcium into mitochondria of soft tissues where it is sequestered in amorphous combination with phosphate, and so its availability to other tissues is remote. Presumably, if strong stimuli, steroid-cascading and hypocalcemia continue, PTH activity in recruiting calcium from tissues would be ineffectual. I conjecture that this is because calcium removed from tissues would be swiftly lost from the blood through the actions of elevated serum cortisol.

Tetany might be caused in sensitive individuals and those already encumbered by extra serum-calcium demands (e.g., pregnant or nursing females). This would be a likely result if ionic pumps began to transfer calcium rapidly from the semifluid and fluid compartments—where non-bone calcium is most plentiful—to the blood. Because of the effects of increased serum steroid concentration, the blood would act as a calcium sink.

The richest source of such calcium is the sarcoplasmic reticulum of the muscle fibers. Removal of calcium from these containers would bring on tetany because their ionic

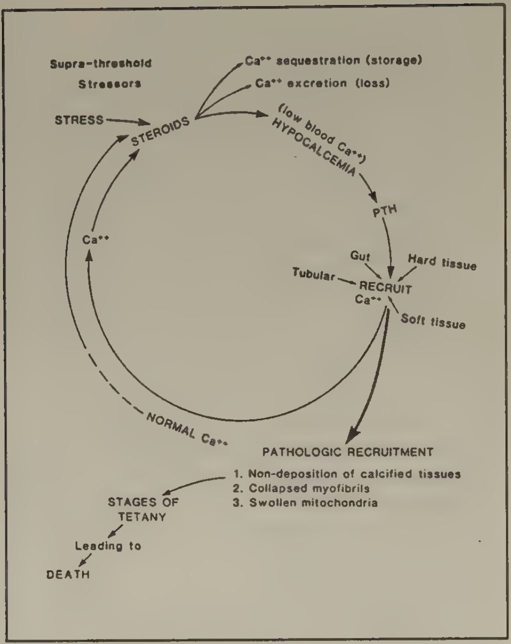
Supra-threshold
Stressors
STRESS
STEROIDS
Ca⁺⁺ sequestration (storage)
Ca⁺⁺ excretion (loss)
(low blood Ca⁺⁺)
HYPOCALCEMIA
PTH
Gut
Hard tissue
Tubular
RECRUIT
Ca⁺⁺
Soft tissue
Ca⁺⁺
NORMAL Ca⁺⁺
PATHOLOGIC RECRUITMENT
1. Non-deposition of calcified tissues
2. Collapsed myofibrils
3. Swollen mitochondria
STAGES OF
TETANY
Leading to
DEATH

Fig. 5 Theoretical model showing systemic calcium ion flow in hypothetical cases of supra-threshold stressors which generate a glucocorticoid flood, hypocalcemia and ineffectual recruitment of body calcium.

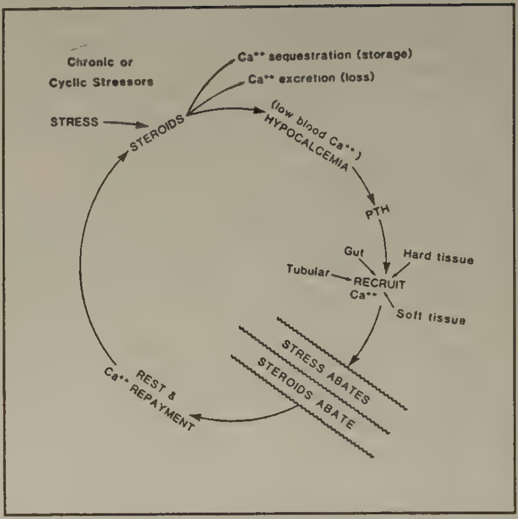
Chronic or
Cyclic Stressors
STRESS
STEROIDS
Ca⁺⁺ sequestration (storage)
Ca⁺⁺ excretion (loss)
(low blood Ca⁺⁺)
HYPOCALCEMIA
PTH
Gut
Hard tissue
Tubular
RECRUIT
Ca⁺⁺
Soft tissue
STRESS ABATES
STEROIDS ABATE
Ca⁺⁺ REST &
REPAYMENT

Fig. 6 Theoretical model showing systemic calcium ion flow in hypothetical cases of chronic sub-threshold or cyclic threshold stressors. In the case of chronic stressors, rest and Ca^{++} repayment is impaired. In the case of cyclic stressors, stress regularly abates, decreasing steroid secretion and promoting Ca^{++} repayment.

calcium is required for muscle contraction. Large-scale removal would invoke paralysis and probable death. Figure 5 represents a theoretical model for such hypothetical cases.

I conjecture further that a less severe situation may occur as in the model in Figure 6. Here, the noxious stimuli would be temporary or cyclic, or perhaps mild and chronic. Presumably this would cause less cortisol to be secreted and released. Marginal or intermittent hypocalcemia would promote low but above-basal secretions of PTH. If cyclic, the stressors would ultimately produce repetitious resorption with full repair in teeth. Chronic stressors, which allowed little recovery time, would ultimately produce large-scale dental resorption with inadequate reparation.

Stress-induced hypocalcemia

If stressors cause the hypersecretion of cortisol into the blood and the elevated serum steroids cause hypocalcemia, then some evidence of these relationships should be found in data related to results in this study and in data reported in accounts by others.

Black bears

Evidence from the black bears suggests that resorption may be due to stresses of winter cold, fasting and cubbing. The bear teeth showed resorption associated with dark-stained annual layers usually followed by complete repair. Montana black bears begin forming the thin, dark cemental layer just before the onset of hibernation (Stoneberg and Jonkel 1966). For these bears, hibernation is a dormant period during which the bear eats nothing and yet it does not conserve body stores by becoming torpid (Pelton 1982) as do true hibernators. In addition to fasting, mature female black bears regularly give birth and begin to suckle (up to four) cubs during hibernation (Pelton 1982). Presumably, resorption is associated with fasting in all individuals except the neonatal cubs (who nurse) and with late pregnancy, parturition and early lactation in mature females.

All specimens with cyclic resorption features show damage, presumably sustained during hibernations. It is completely repaired between winter seasons, just as healthy females of other species fully repay borrowed bone calcium between pregnancies (Braithwaite *et al.* 1970; Toverud and Boass 1979).

Elk

Dental alteration in Rocky Mountain elk may be associated with cyclic stress due to cold, starvation and perhaps exhaustion. Dark-stained layers in cementum and dentine form in winter in the elk (Keiss 1969). Although elk do not hibernate, they do store nutrients for overwintering and normally remain active despite inadequate winter intake of food. Bulls, already predisposed to malnutrition from an active rutting season, and females, increasingly encumbered or pregnancy, may further draw on limited reserves in populations that migrate yearly to and from winter grounds. Yearling cows and bulls entering their second fall may be involved in reproductive activities. Mortality may be high, depending on severity of the winter season, adequacy of stored fat, reproductive state, general state of individual health, and whether the elk are migratory (Peek 1982).

Dolphins

Except for susceptible reproductive females, most tropical dolphins probably have few strong natural stressors, such as starvation, extreme temperatures, inordinate fear and routine physical exhaustion. If that is correct, then repetitious resorption with token repair, as seen in some of the dolphins in the eastern tropical Pacific, may be ultimately caused by unnatural stressors, particularly those associated with the purse-seine fishery. In the fishing operation, chases and sets on dolphins may be of long duration (two to four hours per set), but frequency of sets on the same schools is not known. Myrick *et al.* (1987) have recently shown that spotted dolphins chased and set upon by purse seiners are hypocalcemic, but that captive dolphins acclimated to conditions of captivity and wild dolphins that are slowly captured and handled with a minimum of disturbance to the animals have serum calcium values that are normal for other mammals. Myrick *et al.* (1987) also noted that if capture is somewhat rushed or awkward, a dolphin may easily and quickly experience a drop in serum calcium to below normal levels.

Other cases

Apparent confusion abounds regarding ultimate causes of dozens of nominal diseases or conditions in susceptible mammals, which share in common suites of symptoms indicating hypocalcemic tetany. These fall into four categories including myopathies or paralyses associated with parturition in mammals including humans (parturient paresis), capture of wild animals (capture myopathy), transport of domestic and wild animals (shipping disease) and exhaustion exercises.

In capture and transport myopathy cases where data have been given, I have noticed a consistency of rising cortisols (Franzmann and Thorne 1970) and declining calciums (McAllum 1985; Haigh *et al.* 1977; Chalmers and Barrett 1977; Brannian *et al.* 1981). This is also true for cases describing serum steroid or serum calcium changes in heavily exercised horses (Snow 1982; Snow *et al.* 1983), in endurance race horses (Grosskopf *et al.* 1983; Rose *et al.* 1983; Grosskopf and Van Rensburg 1983; Lucke and Hall 1978; Lucke and Hall 1980; Rose *et al.* 1980), in competing ponies in polo matches (Craig *et al.* 1985) and in laboratory animals and humans in exhaustion-exercise studies (Viru 1985).

In capture myopathy, animals are chased and netted or darted. Depending on the individual and species, they may result in paralysis or death after the animal passes through a series of symptoms that usually include those of early and intermediate tetany. A large percentage of these reports have suggested that metabolic acidosis is a major cause of this condition, but often the condition occurs without acidemic signs. I suggest that an alternative explanation for all such conditions may be in order.

In reports that detail the muscle damage in such lethal myopathies, obliterated z-lines of the sarcomeres and loss of skeletal-muscle striations have been described or illustrated a number of times (Lewis *et al.* 1977; Chalmers and Barrett 1977; Brannian *et al.* 1981). The sarcoplasmic reticula attach near and branch from the z-line areas of sarcomeres. If, as one of the conjectural models indicates (Fig. 5), calcium ions were rapidly removed from the sarcoplasmic reticula by recruitment actions of PTH, it would surely disrupt and rupture muscle cells in the regions of the z-lines in a way much like that described for lethal capture myopathy.

Parturient paresis and related conditions occur in mammals at about the time of parturition. Hypocalcemia is the known cause of this potentially lethal myopathy. However, these conditions have often been explained by suggesting that the calcium needs for the developing fetus, for colostrum formation and to prepare for the onset of normal nursing, suddenly overcome the maternal ability to maintain normocalcemia (Brown *et al.* 1979). In fact, serum cortisol suddenly rises immediately before parturition in many animals (Challis *et al.* 1979; Ellendorff *et al.* 1979; Stone *et al.* 1987). This may be more suggestive that hypocalcemia is caused by the stress of periparturient fear and pain or discomfort rather than any sudden demands made on maternal calcium reserves. This would be especially likely for large mammals in which the calcium burden of pregnancy and lactation are relatively small (Simkiss 1967).

To summarize, I agree with Basson and Hofmeyer (1973) who, in considering only myopathic diseases, suggested that many of the nominal conditions are various species- or stress-specific expressions of the same phenomenon. The present study has developed considerable circumstantial evidence indicating that many of the conditions considered above may result from stress-induced hypercortisolism, hypocalcemia and hyperparathyroidism. It has also strengthened the likelihood that natural and unnatural stressors are ultimate causes of systemic alteration of tooth tissues. Nevertheless, firm data are lacking and direct experimentation and directed study will be necessary before it is possible to fully answer the question: Is tissue resorption and replacement in permanent teeth of mammals caused by stress-induced hypocalcemia?

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Toward calibrating dentinal layers in captive killer whales by use of tetracycline labels

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ABSTRACT

To establish a basis for accurate age estimation of killer whales, growth layer groups (GLGs) were examined in tetracycline-labelled and non-labelled teeth, prepared as decalcified and stained and undecalcified thin sections, from 13 animals with captive histories. Data concerning body length, tetracycline treatments and time in captivity were used in conjunction with labels and GLG patterns to identify annual rates of deposition. For this sample, the annual thickness of dentine deposited in the neck region of a tooth was never less than 700 μm and usually between 800 and 900 μm, even in adults. In this region, a standard measurement aids in identifying the extent of each annual GLG when accessory layers obscure its true boundary layers. Dentine was not readable after about the twentieth GLG, and cementum was usually poorly layered and very thin. Another age determination method should be sought for such cases if data for older age classes of a sample are desired.

INTRODUCTION

The method of age estimation of toothed cetaceans, based on counts of growth layer groups (GLGs, Perrin and Myrick 1981) of tissue in the teeth, was introduced 35 years ago (Nishiwaki and Yagi 1953). Since then GLG counting has become an important procedure when studying the age-related biology of odontocete populations (Scheffer and Myrick 1981; Kasuya 1976, 1977; Myrick *et al.* 1986).

The three most widely used techniques for tooth preparation and examination to estimate age are as follows:

1) Etched half-teeth – acid etching cut surfaces of longitudinally bisected teeth and "reading" dentinal GLGs in relief with reflected light, as a chevron-shaped series of valleys and ridges.
2) Untreated sections – sawing and polishing a thin longitudinal wafer from the center of a tooth and reading the GLG chevrons in transmitted light, as a series of darker and lighter layers.
3) Decalcified and stained (D&S) sections – cutting thin longitudinal sections from the central part of a decalcified whole tooth or central wafer with a freezing microtome, staining sections with hematoxylin and reading GLGs in cementum (along the external margins of the root) as well as in dentine (within the body of the tooth) in transmitted light, as a series of darker and lighter stained layers (See Perrin and Myrick 1981, pp. 3–48; Myrick *et al.* 1983).

Acid etching has been used chiefly for species in which teeth are large, such as sperm whales (Clark *et al.* 1968) and killer whales (Christensen 1982, 1984). Etching is a relatively simple method that produces a coarse relief thought to be adequate for identifying

GLGs in large teeth (Pierce and Kajimura 1981). D&S has been done most often on teeth of dolphins and porpoises because the teeth are small and GLG patterns are fine and difficult to see in acid-etched relief (Kasuya 1976, 1977; Perrin and Myrick 1981). D&S is a more complicated method than producing etched relief (Myrick *et al.* 1983).

The use of untreated sections has had limited success for age estimation (Perrin *et al.* 1976). Untreated sections have been used primarily to study coarse layering in large teeth, such as those of sperm whales (Klevezal and Tormosov 1971) and with ultraviolet light (UV) to examine teeth containing artificially introduced tetracycline labels (Nielsen 1972; Best 1976; Gurevich *et al.* 1981; Klevezal 1981; Myrick 1981; Myrick *et al.* 1984), in which fluorescent traces are lost if teeth are decalcified (Nielsen 1972).

A few published studies of killer whales have included age estimates based on GLG counts (Sergeant, in Caldwell and Brown 1964; Perrin and Myrick 1981; Christensen 1982, 1984). Of these, the latter three studies made counts on a substantial number of teeth and used etched half-teeth exclusively, except for the IWC workshop study (Perrin and Myrick 1981) which also employed one untreated and three D&S thin sections. In addition, the latter three studies indicated the nature of the counts and provided GLG definitions. To date, however, no study of killer whales has included known-age, minimum known-age and tetracycline-labelled specimens. Inclusion of such materials would permit calibration of tissue units with units of real time, as has been done for two other delphinid species, i.e. *Stenella longirostris* (Myrick *et al.* 1984) and *Tursiops truncatus* (Myrick, unpubl. data). Thus, as Christensen (1984, p. 256) stated, "[although] the etched-tooth technique provides clearly defined dentinal [GLGs in killer whale teeth], their interpretation with regard to [absolute age remains] provisional."

Two international meetings of cetacean biologists have indicated that: 1) data are needed as a basis for age determination of killer whales (Perrin and Myrick 1981; IWC 1982); 2) improvement is needed in preparation and examination techniques to age killer whales using the D&S method (Perrin and Myrick 1981); and, in general, 3) known-age, known minimum-age, and tetracycline-labelled (captive) specimens should be studied "for calibration of dentinal layer groups and for cross-calibration of dentinal [and] cemental... layering" (Perrin and Myrick 1981, pp. 39–40). Using teeth and records from all available specimens known to us with captive histories, we have responded to the research recommendations concerning killer whale age determination as suggested above. We here account the methods and results of a study that was conducted to calibrate dental layers in killer whales *(Orcinus orca).*

MATERIALS AND METHODS

The Sample

We used a single tooth from each of 13 killer whales, 12 dead and one live, captured from the wild and held in captivity at U.S. oceanaria for various periods. Ten of the 13 animals had been treated with tetracycline for physical ailments during their captive lives. The teeth were studied in conjunction with data on capture dates, length at capture, therapeutic treatment dates and dates of death (the date of tooth extraction for the live animal) from medical records of varying completeness (Table 1).

Labels

Using reflected UV light, we examined untreated sections from all individuals to identify fluorescent labels corresponding to recorded, as well as unrecorded, tetracycline treatments. By turning the transmitted plain light source on and off while the reflected UV remained on, we were able to locate precisely the positions of the labels within the layering patterns. Following Myrick *et al.* (1984), we photographed labelled regions of untreated sections in UV and plain light separately and in UV and plain light simultaneously to estab-

TABLE 1

*Background data and age estimates of 13 captive killer whales used to calibrate GLGs in the teeth (Origin: A = North Atlantic, P = northeastern Pacific. * = Estimated age at capture based on body length).*

		Capture						Estimates of total age (y) based on:		
No.	*Sex*	*Orgin*	*Date*	*Length cm*	*Age* (y)*	*Extraction or Death*	*Time Captive (y)*	*Capture length and captive time*	*Capture length, captive time, labels and GLGs*	*Captive time and GLGs with and without labels*
001	m	P	11 Mar 67	277	1	23 Sep 78	11.5		12.5	
002	m	P	29 Apr 68	401	?5	5 Dec 70	2.7	7+	10.5	
003	f	P	27 Dec 69	290	1.3	4 Aug 71	1.7			3.0
004	f	P	27 Aug 71	379	4	15 Jun 75	3.8	7.8	6.0	
005	m	P	12 Dec 69	412	?5	20 May 72	2.4		7.4	8+
006	f	P	26 Aug 71	434	5+	28 Sep 77	6.1	12.0		15.0
007	m	P	12 Mar 72	354	3+	1 Dec 74	2.7	6.0		7+
008	f	P	Mar 73	488	<7	22 Oct 77	4.6	12+		19+
009	m	A	12 Oct 77	350	3	2 Aug 81	3.8		7+	
010	f	A	Oct 78	287	1+	21 Mar 82	3.5			5.0
011	f	?	65			29 Aug 71	6.0			12.0
012	m	P	Oct 68	427	5+	Oct 82	14.0			20+
013	f	P	1 Mar 70	335	3	2 Nov 72	2.7		6.0	

lish the positions of labels within GLG patterns (Figs. 1A and 1B).

To make the connection between layers and time, dentinal thicknesses were measured in a standard position in the neck region of each tooth (Fig. 1B). Measurements were made of dentine accumulated between the neonatal line and labels, between each label and between labels and the pulp-cavity margin. Each measurement was made at least three times and averaged. We then matched labels to recorded tetracycline treatments by interpreting distance between labels as corresponding to time between treatment dates, thickness of labels as duration of treatment, and brightness as strength of dose. Each measurement (in μm) was divided by the time elapsed between dates to yield the annual depositional thickness of dentine. Then, measurements from each specimen were totalled and divided by total captive time to get a mean annual depositional rate (Table 2). To mitigate the effects of local variation and measuring error, all values were rounded to the nearest 50 μm. Rounding made the values easy to deal with and, considering the large sizes of the GLGs, made little difference in absolute values.

In four specimens (Nos. 005, 006, 007, 011), treatments had been administered on or shortly after the date of capture. This gave a complete dentinal record of time in captivity from the first label (date of capture) to the pulp-cavity margin (date of death or tooth extraction, Fig. 1C). The number of specimens with a label introduced at capture was expanded from four to six (by adding Nos. 001 and 003) after study of other specimens had shown that, although the earliest labels in the latter two specimens lacked dates, the label distances and positions relative to other structures and labels corresponded in time to the capture dates. (It is not unusual to find poor records of medications given during the first days of captivity to protect newly caught animals during their adjustment – Myrick *et al.* 1984).

GLG Patterns

To obtain the best resolution of layering patterns, D&S sections were prepared from

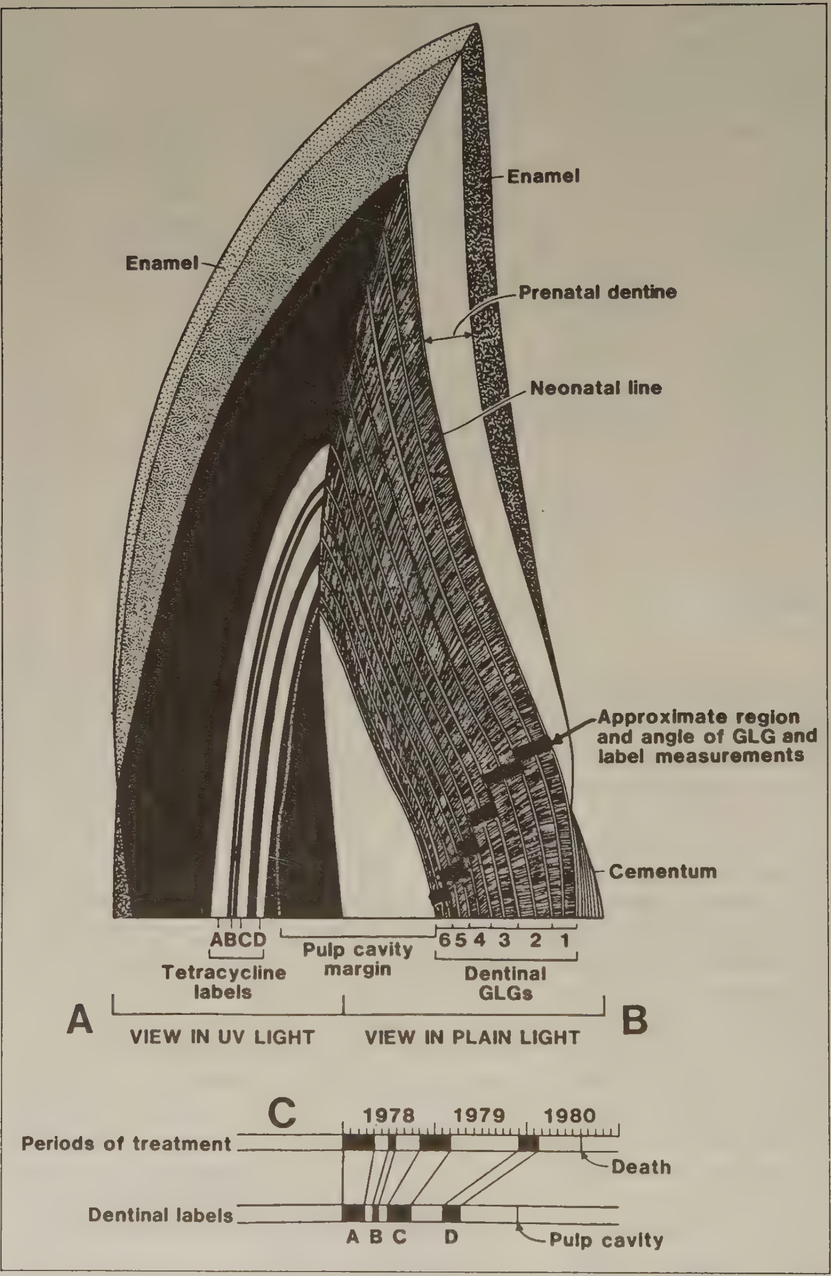
Enamel
Enamel
Prenatal dentine
Neonatal line
Approximate region and angle of GLG and label measurements
Cementum
ABCD
Tetracycline labels
Pulp cavity margin
6 5 4 3 2 1
Dentinal GLGs
A
B
VIEW IN UV LIGHT
VIEW IN PLAIN LIGHT
C
1978
1979
1980
Periods of treatment
Death
Dentinal labels
A B C D
Pulp cavity

Fig. 1. Diagram of tooth thin section from hypothetical captive delphinid (other than killer whale) showing A) tetracycline labels under UV reflected light (left) and B) dentinal GLG patterns under plain transmitted light and standard positions where labels and GLG thicknesses are measured (right). The map C) illustrates the method of identifying labels in a tooth section for which tetracycline treatment dates are known, by comparing relative thickness and spacing of labels with intervals and durations of treatments. (Modified from Myrick *et al.* 1984).

remaining parts of the teeth from which untreated sections were made. This facilitated the comparison of gross GLG patterns, structures and labels seen in untreated sections with GLGs defined in D&S sections.

The basic D&S procedure consisted of making 2-mm-thick wafers from near the center of a tooth with a small saw, decalcifying the wafers in a rapid bone decalcifier, cutting the wafers to fit the microtome stage and then dividing the wafers into 30-μm-thin long sections. Rinses and staining followed procedures by Myrick *et al.* (1983). The stained thin-section pieces were reassembled on glass slides in pure glycerol to prevent shrinkage. A full account of the D&S preparation method for killer whale teeth will be reported elsewhere (Yochem, in prep.).

The remaining parts of several half-teeth were also prepared using the etching technique to compare the GLGs in relief to those seen in D&S section. Results of that comparison have been summarized earlier and will be described fully in a forthcoming report (Yochem, in prep.).

Calibration

In calibrating dentinal layers, our primary objective was to define the killer whale annual GLG by imposing the time data upon the layering patterns and vice versa. To do this, we first identified repeating layering patterns (pattern GLGs) in D&S sections. Then using direct measurements from natural markers and superimposed photographs of tooth tissues, we located the same regions in untreated sections, enveloped by series of dated labels (Fig. 2). From the elapsed time between labels represented in the untreated section, we then determined the time interval of the pattern of GLGs identified in D&S sections. Finally, we compared results from all study specimens with adequate labels to define the annual GLG, both visually and in terms of dentinal thickness.

Our GLG definition was tested by using it on the specimens to estimate their ages. The counts of annual GLGs were used to determine, in the blind, the ages of specimens for which total or minimum age estimates were already available. These earlier estimates had been derived from age based on length at capture plus total time in captivity. As a basis for age-at-length estimates, we adopted Bigg's (1982) interpretation that a body-length of 9 feet (274 cm) represents a one-year old, and that length increases by about 1.2 feet (35.6 cm) per year to a length of 16 feet (488 cm) (Table 1).

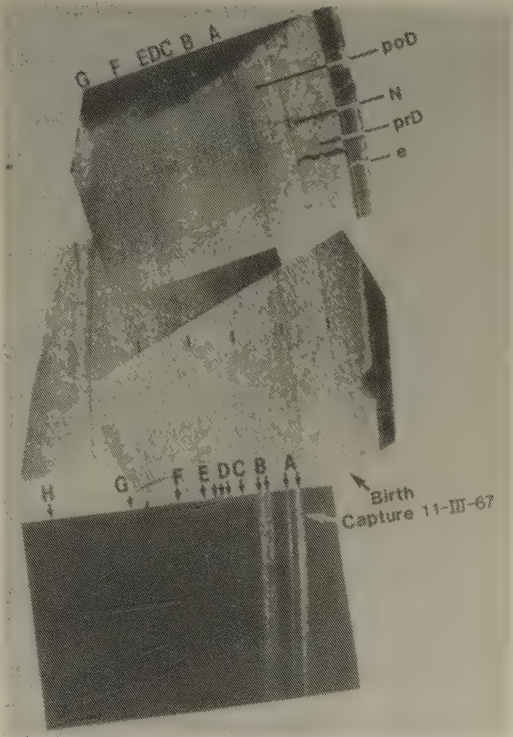

Fig. 2. Matched UV and plain-light photographs of an untreated tooth section of killer whale No. 001, showing the location of tetracycline labels (lettered arrows). The right-hand label in group A was introduced at capture and is separated from the neonatal line (N) by one GLG. GLGs are about 900 μm thick and are shown here bounded by vertical bars. The left-hand label of group B, label C and label F were introduced 1.0, 0.6 and 1.9 years apart, respectively. Dates of other labels were not identified (see Table 2). e = enamel, PoD = postnatal dentine, PrD = prenatal dentine.

Our final objective was to compare GLG counts from patterns in the cementum with those made in dentine (in D&S sections) to evaluate the possiblity of using cementum reliably in age estimation.

A special problem emerged in analyzing the labels for specimen No. 001 (Tables 1 and 2, Fig. 2). This whale had been captured as a one-year old (9 feet 1 inch or 277 cm) and held in captivity for 11.5 years. During that time many tetracycline treatments were given, but only five treatment dates were preserved in its medical records. By studying dentinal de-

TABLE 2

Life history events and tetracycline treatments accounting for spacing between structures and labels in killer whale teeth used to define annual depositional rates (see Materials and Methods). (NNL = *neonatal line, formed at birth;* PC = *pulp-cavity margin or label at pulp-cavity margin, indicating end of tooth record);* A: *North Atlantic;* B: *northeastern Pacific;* d: *day(s);* y: *year(s);* * *indicates age estimated from body length at capture).*

Spec. No.	Event	Date* from length at capture	Treatment period dose	Structure or Label			Elapsed time (y)	Distance (µm)	Rate (µm/y)
				With data	No data but used	No data not used			
001	Birth	~ Mar 66*		NNL					
	Capture	11 Mar 67	unknown		A		~1.0*	900	900
		27 Mar 68	unknown	B			1.0	800	800
		17 Nov 68	13d – unknown	C			0.6	500	850
		unknown				D			
		unknown				E			
		28 Oct 70	5d – unknown	F			1.9	1600	850
		unknown				G			
		unknown				H			
		21 Apr 76	8d – 75g/d	I			5.5	5000	900
		13 Sep 78	3d – 30g/d	(PC)					
	Death	23 Sep 78		PC			2.4	2000	850
		total time captive					11.5		
		total age and average rate					12.5*		850
002	Birth			NNL					
	Capture	29 Apr 68	unknown		A		7.5	7000	
		5 Jan 70	80d – 20g/d	B			1.7	1600	950
		unknown				C			
	Death	25 Dec 70		PC			1.0	850	850
		total time captive and average rate					2.7		900
		total age					10.7		
003	Birth	Jul 69*		NNL					
	Capture	27 Dec 69							
		5 Jan 70	unknown – 20g/d	A			1.3*	1100	850
		22 Apr 70	unknown – 20g/d	B			0.3	250	850
	Death	4 Jul 71		PC			1.3	1250	950
		total time captive					1.7		
		total age and average rate					3.0*		850
004	Birth			NNL					
	Capture	27 Aug 71	unknown		A		2.3	2100	900
			unknown			B			
			unknown			C			
	Death	15 Jun 75		PC			3.8	3200	850
		total time captive and average rate					3.8		850
		total age					~6.0		
005	Birth			NNL					
	Capture	12 Dec 69							
		6 Jan 70		A			5.5*	5150	950
	Death	20 May 72		PC			2.4	2000	850
		total time captive and average rate					2.4		850
		total age					~8.0*		
006	Birth			NNL					
	Capture	26 Aug 71							
		18 Jun 72	12d – unknown	A			0.8	8100	
		7 Jul 72	10d – 38g/d	A					

Table 2 (continued)

Spec. No.	*Event*	*Date* from length at capture*	*Treatment period dose*	*Structure or Label*			*Elapsed time (y)*	*Distance (µm)*	*Rate (µm/y)*
				With data	*No data but used*	*No data not used*			
		12 Sep 77	1d – 30mg/d	B	(PC)				
		15 Sep 77	7d – various	B	(PC)				
	Death	28 Sep 77		PC			6.1	5000	800
		total time captive and average rate					6.1		800
		total age					15.0		
007	Birth			NNL					
	Capture	12 Mar 72							
		21 Apr 72	4d – 60g/d	A			0.1		
		25 Mar 74	4d – 10g/d	B			1.9	1700	900
		21 Sep 74	3d – 20g/d	(PC)					
	Death	21 Dec 74		PC			0.7	650	900
		total time captive and average rate					2.7		900
		total age					7.0		
008	Birth			NNL					
	Capture	Mar 73							
	Death	22 Oct 77		PC					
		total time captive					4.6		
		total age					19+		
009	Birth			NNL					
	Capture	12 Oct 77					3.0*		
		23 Jun 80	24d – 20g/d	A			5.7	4950	850
		22 Jul 81	6d – 40g/d	B	(PC)				
	Death	2 Aug 81		PC			1.1	1000	900
		total time captive					3.8		
		total age					7+		
010	Birth	summer 77*		NNL					
	Capture	Oct 78					1+*		
		27 May 79	3mo – 10g/d	A			0.6		
		20 Mar 82	1d – 20g/d	B	(PC)				
	Tooth Extraction								
		21 Mar 82		PC			2.8	2400	850
		total time captive					3.4		
		total age					5.0*		
011	Birth			NNL					
	Capture	?-65							
		20 Dec 65	8mo – various	A					
		7 Jan 67	19d – unknown	B			1.0	850	850
		3 Jul 67	17d – —	C			0.5	400	800
		30 Aug 67	19d – —	C					
		10 Oct 67	27d – —	C					
		24 Feb 68	7d – —	D			0.6	1000	1650
		3 Mar 68	4d – —	D					
		30 Mar 68	14d – —	D					
		18 Aug 68	30d – —	E			0.4	350	850
		27 Sep 68	31d – —	E					
		31 Dec 68	48d – —	E					
		24 Jul 70	9d – —	F			1.9	1550	800
	Death	29 Aug 71		PC			1.1	900	800
		total time captive and average rate					5.7		900
		total age					12.0		

Table 2 (continued)

Spec. No.	*Event*	*Date* from length at capture*	*Treatment period dose*	*Structure or Label*			*Elapsed time (y)*	*Distance (μm)*	*Rate (μm/y)*
				With data	*No data but used*	*No data not used*			
012	Birth			NNL					
	Capture	Oct 68							
	Death	Oct 82		PC					
		total time captive					14.0		
		total age					20+		
013	Birth			NNL					
	Capture	1 Mar 70							
	Death	2 Nov 72		PC					
		total time captive					2.7		
		total age					5.7		

position rates of the other specimens and assuming that No. 001 had a similar rate and pattern, we were able to predict where the dated treatments should occur in the layered dentine. In this way it was possible to sort out the dated from the non-dated labels. As it turned out by this assumption, the preserved dates corresponded in time with the dentinal spacing of labels. Moreover, using the distance between label A and the neonatal line on one side and the distance between label A and the second label group (group B) on the other, we determined that the most external label in label A group (Fig. 2) was introduced at about the time the yearling was captured. The dentinal pattern deposited in its first year (in the wild) could then be defined.

RESULTS

Dentinal GLG Pattern

In D&S thin section, the GLG pattern in our sample seemed deceptively simple. Each GLG consisted of a broad, lightly stained layer containing a varying number of thin dark-stained (accessory) layers. The thin layers near the middle bisected the broad layer subequally, while those at the sides separated it from other broad layers contiguous with it (Fig. 3, lower left region). However, in many areas of the sections, the more centrally positioned accessory layers resembled boundary layers so closely that we could not decide whether the GLG to be counted was double-layered or single-layered (Fig. 3, upper right region). It was only through calibration of dentine that the composition of the annual GLG was defined.

Direct measurements of GLGs in D&S sections of all specimens showed that usually single layered GLGs were about half the value (about 450 μm) of the double layered GLGs, which were typically between 800 and 900 μm thick. Repeated measurements of all GLGs in tooth neck regions indicated that although values fell below 800 in some of the last-formed double layered GLGs of the three oldest specimens (Nos. 006, 008, 012 – Table 2), none was less than 700 μm thick.

GLG Calibration

Mean annual rates of dentinal deposition for 10 of the 13 specimens in which they could be calculated from labels are presented in the right-hand column of Table 2. These averages fell within the same range of values (800–950 μm) as the individual annual thickness in specimens that have numerous labels separated by about one year (Nos. 001, 002, 003, 011). An exception to this rate was found only in specimen No. 011. Here, a rate of 1650 μm/year was calculated for a thickness of 1000 μm deposited over five months. We were unable to explain this apparent anomaly. We concluded, nevertheless, that the data in Table 2 overwhelmingly supported the use of the double-layered GLG greater than 700 μm thick (in the neck region) as a mean annual dentinal unit.

Ages from Calibrated GLGs

If this definition of an annual GLG is accurate for all killer whales in our sample, then a count of annual GLGs in the specimens should agree with their estimated ages from capture length/age and time in captivity. The estimates based on capture length and time in captivity are compared to those from GLG counts independent of age-at-length data in Table 1.

In five of the 12 specimens with capture length (Nos. 002, 004, 006, 007, 008), there was a difference of > 1.0 to 7.0 years between age estimated from length plus captive time and estimates made from GLG counts. All five were more than 11.5 feet (350.5 cm) long at capture; two of them were more than 14 feet (488 and 434 cm) long. Only in the case of No. 004 was the GLG age estimate less than the age/length estimate (6.0 years vs. 7.8 years).

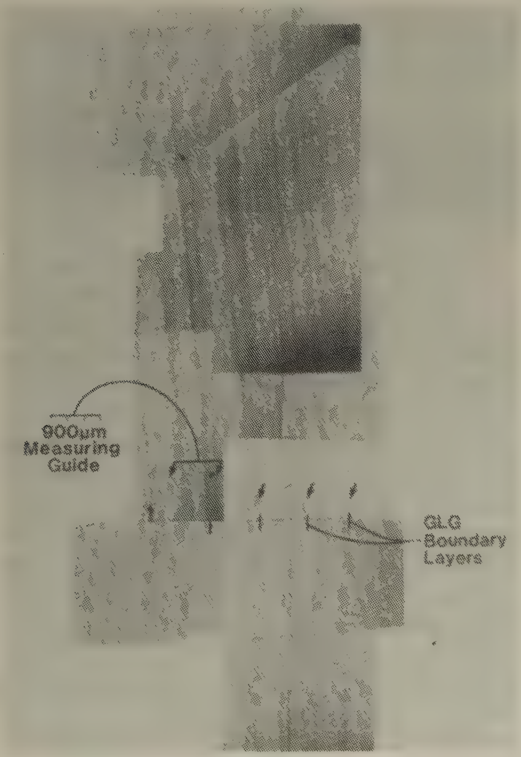

Fig. 3. D&S section of killer whale tooth showing annual GLGs in the region of the tooth neck. Each GLG is characterized by a broad, lightly stained layer, bounded and bisected by a variable series of closely-spaced, thin, dark stained layers. Note, especially in the upper right-hand area, how boundary layers become confused. Because the GLGs are usually between 800 and 900 μm thick, a standard measured scale helps in identifying the extent of annual deposition.

For two reasons we concluded that the GLG estimates were closer to the actual age than the body-length plus captivity age estimates. First, in the other seven specimens, almost all smaller and easier to age at capture than the five, the two estimates were within a year of each other. Second, GLG thickness varied little from year to year. Thus, total thickness of dentine deposited between birth and capture could be divided by about 900 μm to get an approximate age at capture (Table 2). When this could be done (i.e. when a physical capture point could be identified in the tooth) for four of the other five specimens (Nos. 002, 004, 006, 007), age at capture plus time in captivity was within a year of the age estimated from GLG counts (Tables 1 and 2).

The maximum age estimated from dentinal GLG counts for one specimen was about 21 years; the next oldest specimen was a little more than 19. In both specimens, additional but irregular and unreadable dentine occurred near the pulp cavity. Because it had no structural resemblance to the GLG, we found no basis for increasing the age estimates. Neither specimen had age-at-capture estimates or tetracycline labels. Thus, it is possible that both of these specimens were somewhat older than the age estimates given.

Cemental GLGs

Cementum of killer whales that we examined was very thin and poorly layered in D&S sections (Fig. 4). Where tetracycline labels could be detected in the cementum, no consistent correspondence could be found of GLGs before and after the cemental labels with GLGs between labels in the dentine.

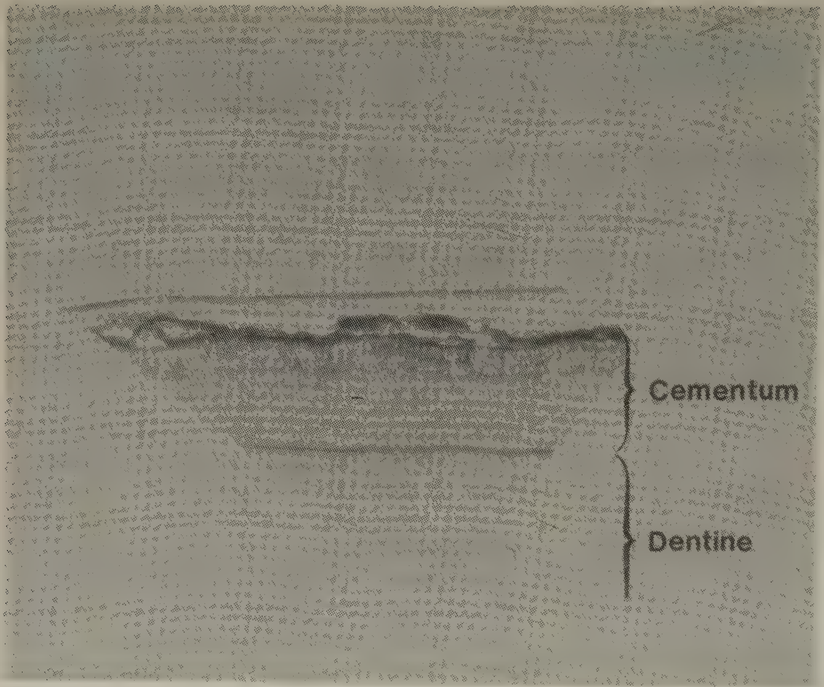

Fig. 4. D&S thin section of cementum of No. 001, a 12.5-year-old killer whale, showing GLGs. Cementum was very thin and poorly layered in the samples examined.

DISCUSSION AND CONCLUSIONS

Our study has shown that, with proper records and specimens, tetracyline can be used to calibrate killer whale dentine. The sample we used indicated consistently that in D&S thin section an annual GLG is made up of a broad, lightly stained layer bounded and bisected by a variable number of thin, dark-stained accessory layers. Usually, this annual unit, measured in the region of the tooth neck, was between 800 and 900 μm thick. However, it was never less than 700 μm thick, even in mature animals. We suggest that where accessory layers blur GLG boundaries (Fig. 3) a standard measure could be used to identify the annual unit. Although a 900-μm measurement was used as a guide in this paper, we think that any scale capable of delineating clearly between 450 μm and 700 μm would be useful.

The finding that GLG thickness tended to be uniform throughout the dentine (Table 2) is a dramatic departure from the pattern established for other delphinid species, as depicted in Figure 1B. For non-killer whales, each GLG tends to be thinner than that deposited in the previous year (Best 1976; Gurevich *et al.* 1981; Myrick *et al.* 1983, 1984). The difference in depositional patterns may be connected with functional difference between the biting teeth of killer whales and the prey-manipulation teeth of most smaller delphinids. Whatever the case, it should be kept in mind that we could not test the hypothesis that uniformly thick GLGs occur in animals older than 20 or so years of age. Teeth from animals more than 20 years of age should be studied to resolve this question.

Because of the difficulty in reading cemental GLGs and in linking them in some consistant manner to dentinal GLGs, we view as unreliable the method of using cemental layers alone for age determination.

Our sample yielded two specimens which, based on the dentinal GLG counts, were estimated to be approximately 20 years old. Additional but disordered dentine had been accumulated in these specimens subsequent to the formation of the GLGs, possibly indicating older ages. Thus, new methods for estimating age in very old individuals should be explored.

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"Bone Softening," a Practical Way to Utilize Small Fish

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Introduction

Many of the fishery resources available on the U.S. west coast are being harvested at maximal levels. To increase fisheries production, there is a need to turn to presently underutilized species. Reasons for not using certain fishes are varied, but small size is frequently cited as one of the chief impediments. This is principally because most Americans, and indeed people throughout much of the world, are accustomed to eating boneless fillets of fish, and small fish are usually uneconomical to debone or fillet.

Even in Japan, where per-capita fish consumption is about 5 times that of the United States, small fishes present problems in utilization. Thus, the enormous catch of sardines there (more than 4 million tons in 1986) is used primarily for fish meal rather than for direct human consumption. Looking for ways to increase direct consumption of sardines and other small fishes, Japanese researchers considered various alternatives. One of the more successful products developed was "bone-softened" fish, which utilized small fish that were "dressed," i.e., head, tail, and viscera removed, but with skeletal bones, spines, and some scales left intact. The obvious advantages of using dressed fish rather than fillets are higher yield and lower processing costs. A further advantage may be in increased nutritional value, as bone is a good source of many essential minerals, particularly calcium.

In the fall of 1986, JAC Creative Foods, Inc.[1], Los Angeles, Calif., and the West Coast Fisheries Development Foundation, Portland, Oreg., obtained a Saltonstall-Kennedy fisheries development grant from the National Marine Fisheries Service to study ways to increase utilization of certain California fishes. One aspect of this project was to study bone softening techniques using small species of fish that are abundant off the California coast. The principal objectives were to learn if hard parts (bones, scales, and spines) of these species could be softened so that they would be undetectable when eaten, and to attempt to manufacture products made with bone-softened fish that are palatable to American tastes. This paper presents findings of that study to provide the fishing industry as well as consumers with information about the production and consumption of bone-softened fish.

Materials and Methods

Most of the fish used in this study were caught with bottom trawls and were provided by fishermen from Monterey and Morro Bay, Calif. Species included shortbelly rockfish, *Sebastes jordani*; Pacific sanddab, *Citharichthys sordidus*; white croaker, *Genyonemus lineatus*; plainfin midshipman, *Porichthys notatus*; rex sole, *Glyptocephalus zachirus*; English sole, *Parophrys vetulus*; Dover sole, *Microstomus pacificus*; and ratfish, *Hydrolagus colliei*. Additionally, samples of so-called "small pelagic species" (i.e., jack mackerel, *Trachurus symmetricus*; Pacific mackerel, *Scomber japonicus*; and Pacific sardine, *Sardinops sagax*) caught off southern California with roundhaul nets, were obtained from wholesale fish dealers in Los Angeles. Specimens of yellowfin tuna, *Thunnus albacares*; and goosefish, *Lophius americanus* (often called "monkfish"), which were used in two comparative experiments were also purchased at a wholesale fish market. All fish except the last two and the ratfish were smaller than 28 cm (11 inches) in total length.

Processing operations and most evaluation procedures were carried out at two fish processing plants in Los Angeles, JAC Creative Foods and Yamasa Enterprises. For each experiment, frozen fish were thawed at room temperature, then measured and weighed. They were then dressed, and the visceral cavity scrubbed clean. After being weighed a second time to determine the amount of waste, several fish were lined in a single layer, wrapped in aluminum foil[2], and cooked in a laboratory-sized autoclave. The cooker was a Barnstead Benchtop Autoclave, with a chamber 39×25 cm (15½×10 inches), and a capacity of around 1.15 kg (2.5 pounds) of material. Pressure within the chamber was dictated by the experimental temperature, i.e., the pressure was constant for each chosen cooking temperature: At 116°C, the pressure was 0.7 kg/cm^2 or k.s.c. (240°F, 10 pounds/inch^2 or p.s.i.); at

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[1] Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2] This was necessary only because the small autoclave used in this study could not accommodate juices that emanated during processing. Commercial operations would utilize open racks.

121°C, 1.05 k.s.c. (250°F, 15 p.s.i.); at 127°C, 1.40 k.s.c. (260°F, 20 p.s.i.); at 132°C, 1.75 k.s.c. (270°F, 25 p.s.i.). Fish prepared for outside evaluation were cooked in an autoclave that was similar, but with slightly greater capacity.

Experiments were also conducted to attempt to improve the texture and moistness of bone-softened fish. These trials entailed pretreatment of the fish by soaking dressed fish overnight in cold salt (sodium chloride) brine solution of various concentrations. The samples and solutions were kept refrigerated at about 5°C (41°F). Other treatments tried were addition of varied amounts of citric acid or sodium tripolyphosphate (TPP) to vary the pH level of the soaking solution.

To remove the "fishy" odor of some species, we used extracts of powdered Japanese green tea in salt brine solution. Various amounts of tea were steeped in 800 ml (1.06 quarts) of tap water at 95°C (203°F) for 30 minutes. The tea solution was then filtered through cheese cloth and enough water was added to make up a volume of 1 liter. Test fish were soaked in the tea solution overnight. About 1.2 kg (2.6 pounds) of fish were treated in 1 liter of solution. Different species were kept in separate containers.

The cooked samples were drained, and allowed to cool. For most tests the extent to which the bones were softened was determined by having a number of persons (usually five, including the first two authors and three plant personnel) eat the samples of processed fish and report whether the hard parts were: 1) Detectable when eaten, 2) slightly noticable when eaten, or 3) undetectable when eaten. A fourth, nonorganoleptic measure was also used: 4) Bones crumble easily after slight finger pressure. Both items 3 and 4 were considered desirable endpoints of our experiments. Evaluation of other attributes such as texture and moistness was made by the first two authors.

Chemical analyses of bone-softened shortbelly rockfish and jack mackerel were carried out by a private firm, Michelson Laboratories, Inc., 6280 Chalet Drive, Commerce, CA 90040. Samples of both species were dressed, then soaked overnight in brine solution (1.5 percent salt for shortbelly rockfish and 2 percent for jack mackerel) which also contained 0.25 percent tea solution. In addition, the soaking solution for jack mackerel included 0.25 percent TPP. One liter of solution was used for each 1.2 kg of fish. After soaking, the fish were cooked in an autoclave at 121°C and 15 p.s.i. for 40 minutes. For each analysis, two fish of each species were ground and blended together.

Formal organoleptic evaluation of bone-softened shortbelly rockfish and jack mackerel was conducted by a taste panel composed of members of the staff of the Utilization Research Division, NMFS Northwest and Alaska Fisheries Center, Seattle, Wash. The panel members were trained to conduct such tests.

Results

Bone Softening

Effects of Cooking Temperature and Pressure

Ten species of fish were cooked for a constant time (40 minutes) at varied temperatures and pressures to learn the effects of these treatments on softening bones, scales, and spines. Of the four temperatures and pressures used, the lowest (116°C; 10 p.s.i.) was sufficient to soften the bones of most fish satisfactorily (Table 1). At 121°C, only the midshipman failed to attain a good score (3 or 4). Increasing temperature (and pressure) clearly resulted in greater softening of hard parts.

Vertebral bones of shortbelly rockfish and white croaker were somewhat more difficult to soften than the other fishes. Bones of the small pelagic species (mackerels and sardines) were easily softened, as were those of small flatfish (rex, Dover, and English soles) and Pacific whiting.

Effects of Cooking Temperature, Pressure, and Time

Samples of jack mackerel whose average weight was around 104 g (0.23 pound) were cooked at 110°, 116°, and 121°C for 25-50 minutes. Prolonged cooking time did not result in increased softening of bone (Table 2). On the other hand, increasing the cooking temperature from 110° to 116° and 121°C markedly softened the bones, as was found in the first experiment. At 116°C a cooking time of 25 minutes was sufficient to soften bones of jack mackerel.

Effects of Fish Size

Samples of Pacific mackerel and shortbelly rockfish were separated into three size groups and cooked at three temperatures for a constant time. The results (Table 3) indicated that within the

Table 1.—Extent of softening of bone with varied temperatures and pressures. Cooking time was 40 minutes. Numerals are average scores of five tasters, and correspond to: 1 = bone detectable when eaten, 2 = barely detectable when eaten, 3 = not detectable when eaten, and 4 = bone crumbles easily when rubbed between the fingers.

Species	Cooking temperature (°C) and pressure (p.s.i.) 116° (10)	121° (15)	127° (20)	132° (25)
Plainfin midshipman	1	2	3	4
White croaker	2	3	4	4
Shortbelly rockfish	2	3	4	4
Pacific whiting	3	4	4	4
Pacific mackerel	3	4	4	
Pacific sardine	3	4	4	
Jack mackerel	3	4	4	
Dover sole	3	4	4	
English sole	3	4	4	
Rex sole	3	4	4	

Table 2.—Effects of cooking time, temperature and pressure on softening bones of jack mackerel. The scoring system is the same as that given in Table 1.

Cooking time (minutes)	Cooking temperature (°C) and pressure (p.s.i.) 110°C (5)	116°C (10)	121°C (15)
25	2	3	4
30	2	3	4
45	2	3	4
50	2	3	4

Table 3.—Effects of fish size and cooking temperature on extent of bone softening. Cooking time was 45 minutes. The scoring system is the same as that used in Table 1.

Species	Fish size (total weight)	Cooking temp. (°C) 110°	116°	121°
Pacific mackerel	Lg. (580 g; 1.28 lb)	2	3	4
	Med. (255 g; 0.56 lb)	2	3	4
	Sm. (167 g; 0.37 lb)	2	3	4
Shortbelly rockfish	Lg. (295 g; 0.65 lb)		1	3
	Med. (205 g; 0.45 lb)		1	3
	Sm. (100 g; 0.22 lb)		1	3

range of sizes tested, fish size was not related to cooking temperature (110°, 116°, and 121°C) with respect to degree of softening of bone. The minimum temperature required was the same for large as well as small individuals. Apparently the specific composition of the bone was more important than fish size in determining whether the bones became soft.

Minimum Cooking Temperatures

Cleaned vertebrae of nine species were cooked at various temperatures for 30 minutes to learn the minimum temperature necessary to soften vertebrae. As before, the test samples were eaten (in this test only by the first two authors) and given a numerical score correlated with the tasters' ability to sense the texture of bone. The vertebrae were also rubbed between the fingers to determine softness. Tuna vertebrae were the most difficult to soften and goosefish vertebrae were the easiest (Table 4). A cooking temperature of 121°C was sufficient to soften bones of nearly all species tested. Shortbelly rockfish bones required a slightly higher temperature to attain a satisfactory degree of softness.

To further study the relationship between bone composition and cooking time needed to soften the bone, the vertebrae of several species of fish were boiled and thoroughly cleaned and dried, and sent to Michelson Laboratories for analyses of chemical composition. Results of the analyses of calcium and nitrogen content of the bone are given in Table 5, along with the minimum temperature needed to soften the vertebae (from Table 4). No correlation between calcium or nitrogen content and the amount of heat necessary for softening bone was evident. English sole vertebrae had the highest calcium content, yet a relatively low temperature was sufficient to soften it. Also, shortbelly rockfish and goosefish bones were similar in calcium content, but the latter's vertebrae were much more easily softened.

Table 4.—Minimum temperatures needed to soften vertebrae of fishes. After most flesh was removed, segments of vertebrae were cooked for 30 minutes in an autoclave.

Species	Min temp. (°C)	Score	Comments
Yellowfin tuna	>127°	1	Bone only slightly softened
Shortbelly rockfish	>121°	2	At 121°C slightly gritty
Pacific sardine	121°	3	
Dover sole	121°	3	
Pacific mackerel	>116°	2	At 116°C slightly gritty
English sole	>116°	2	At 116°C slightly gritty
Jack mackerel	116°	3	
Ratfish	110°	3	
Goosefish	<110°	4	At 110°C bone crumbles easily

Table 5.—Calcium and nitrogen content (percent of total vertebral weight) of vertebrae of some fishes, and the minimum temperature necessary to soften bone. Time of cooking in the autoclave was 30 minutes.

Species	Calcium (Ca)	Total nitrogen (N)	Ca/N	Min temp. (°C)
Yellowfin tuna	21.5%	4.42%	4.86	>127°
Shortbelly rockfish	18.5	2.67	6.93	>121°
Dover sole	14.8	2.46	6.02	121°
Pacific mackerel	13.7	2.29	5.98	>116°
English sole	26.1	2.96	8.82	>116°
Ratfish	7.5	9.71	0.77	110°
Goosefish	17.5	5.75	3.04	<110°

Table 6.—Effect of tea concentration on deodorization of Pacific sardine and jack mackerel. Fish were tested organoleptically after being soaked in the tea solution overnight, then cooked for 40 minutes at 121°C.

Grams of tea in 1 liter of water	Pacific sardine	Jack mackerel
0[1]	Very fishy	Fishy
2	Slightly fishy	Slightly fishy
2.5	No fishy odor	No fishy odor
3	No fishy odor	No fishy odor
5	No fishy odor	No fishy odor
10	No fishy odor, but slight tea odor	No fishy odor, but but slight tea odor

[1] Control

Table 7.—Effect of citric acid in reducing ammonia odor of bone-softened fish. Dressed fish were soaked in chilled 2.5 percent brine solutions overnight, then cooked for 30 minutes at 121°C.

	Citric acid concentration (%)		
Species	0.0	0.1	0.3
Shortbelly rockfish	Slight ammonia odor	No ammonia odor	No ammonia odor
Pacific whiting	Ammonia odor	Slight ammonia odor	No ammonia odor

Deodorization

Preliminary tests showed that solutions of Chinese black tea and oolong tea and Japanese green tea were all effective in deodorizing the flesh of small pelagic species. However, we found that Chinese teas imparted a noticably dark stain on the fish flesh, so their use was discontinued. After the fish were soaked overnight in green tea solution, they were cooked at 121°C for 40 minutes. The effects of soaking fish in various concentrations of green tea solutions on the flesh of Pacific sardine and jack mackerel are given in Table 6. An amount of 2.5 g of green tea in 1 liter of water (2.5‰) was sufficient to deodorize at least 1 kg of small pelagic species. When a tea solution of 10‰ was used, an odor and taste of tea was imparted to the flesh.

When cooked in an autoclave, bottomfish were inherently less "fishy-smelling" than small pelagic species. Both shortbelly rockfish and Pacific whiting emitted a slight ammonia odor, however, and the odor was even stronger in midshipman. White croaker and flatfish had a slight but unobjectionable odor. To reduce the ammonia odor in shortbelly rockfish and Pacific whiting we tried a treatment of citric acid solution. Dressed fish were soaked overnight in chilled 2.5 percent brine solutions containing citric acid, then cooked in the autoclave for 30 minutes at 121°C. Organoleptic evaluation of the cooked fish revealed that a 0.1 percent solution was sufficient to remove the ammonia odor in shortbelly rockfish, while a 0.3 percent solution was required for Pacific whiting (Table 7).

Texture and Moistness

Treatments tested for improving texture and moistness of bone-softened fish included variations in cooking temperature, pH level of the cooked flesh, and salt concentrations of brine solutions. The flesh of jack mackerel soaked overnight in a 2 percent salt solution before cooking was juicy and firm compared to the control (no salt) which was watery and soft (Table 8). A 1.5 percent solution was not effective, while a 3.0 percent salt solution resulted in drier flesh

Table 8.—Effects of different concentrations of salt solutions on texture and moistness of bone-softened fish. The dressed fish were soaked in the solutions overnight, then cooked at 121°C for 40 minutes.

Amt. of salt (%)	Jack mackerel	Pacific sardine	Flatfish
0[1]	Watery Soft	Watery Soft	Watery Soft
1.5	Watery Soft	Watery Somewhat firm	Watery Somewhat soft
2.0	Moist Firm	Somewhat watery Firm	Somewhat mushy
2.5	Moist Firm	Moist Firm	Somewhat mushy
3.0	Dry Firm	Somewhat dry Firm	Mushy

[1] Control.

Table 9.—Texture and moistness of bone-softened fish at varied cooking temperatures. Fish were soaked in 2.5 percent salt solution overnight, then cooked for 40 minutes in an autoclave.

	Characteristics of cooked flesh at specified cooking temperatures		
Species	116°C	121°C	127°C
Pacific sardine	Moist Somewhat soft	Watery Firm	Watery Firm
Jack mackerel	Moist Firm	Dry Firm	Dry Firm
Shortbelly rockfish	Moist Firm	Moist Somewhat soft	Dry Soft
Flatfish	Moist Somewhat firm	Watery Mushy	Watery Mushy

Table 10.—Effect of pH adjustment on texture and moistness of bone-softened fish. Fish were soaked overnight in 2.5 percent salt brine solution, and citric acid (CA) or sodium tripolyphosphate (TPP) was used to adjust pH. Fish were then cooked at 121°C for 40 minutes in an autoclave.

	Characteristics of cooked flesh			
Treatment	Jack mackerel	Pacific sardine	Dover sole	Pacific whiting
Control (2.5% salt)	pH 6.31 somewhat dry; firm	pH 6.15 somewhat dry and watery	pH 6.75 mushy and watery	pH 7.11 soft; somewhat watery
+0.3% TPP	pH 6.51 moist; firm	pH 6.34 moist; somewhat soft	pH 6.95 very mushy	
+0.1% CA			pH 6.66 somewhat soft; moist	pH 7.02 somewhat soft and watery
+0.2% CA			pH 6.60 somewhat firm; moist	pH 6.85 firm; somewhat dry
+0.3% CA	pH 5.80 very dry; firm	pH 5.67 dry; firm		

and was judged to be not as good as that prepared with a 2.0 percent salt solution. Pacific sardine required a 2.5 percent salt brine to produce moist and firm flesh. The flesh of several species of flatfish did not improve with the addition of salt, however, and in fact the texture was markedly worsened as more salt was used.

To test the effects of cooking temperature, dressed fish were soaked overnight in a 2.5 percent salt solution, then cooked separately at three levels of heat and pressure for 40 minutes. The lowest temperature used (116°C) generally resulted in the best texture and moistness in the flesh of the fish tested (Table 9). The flesh qualities of all species of flatfish were significantly better when cooked at 116°C. Unfortunately, somewhat higher temperatures are needed to soften the bones of some species (Table 1).

To learn the effects of pH on texture and moistness of bone-softened fish, we soaked several dressed fish overnight in solutions that contained 2.5 percent salt, and either citric acid or sodium tripolyphosphate (TPP), then cooked the fish at 121°C for 40 minutes. The pH of the cooked fish was then measured and the fish tested organoleptically. The results (Table 10) indicated that addition of 0.3 percent TPP effectively increased moistness in jack mackerel and Pacific sardine, but caused Dover sole flesh to become very mushy. When the pH was lowered by addition of citric acid, the flesh of jack mackerel and Pacific sardine became too dry. Conversely, the same treatment caused an improvement in texture of Dover sole and Pacific whiting and there was also a noticable improvement in reduction of objectionable odor.

Proximate Analysis

The compositions of dressed and cooked shortbelly rockfish and jack mackerel caught in October are given in Table 11. Prior to cooking, shortbelly rockfish was soaked overnight in 1.5 percent and jack mackerel in 2.0 percent brine solutions. The percentages of total protein, 22.45 percent and 25.71 percent for shortbelly and jack mackerel respectively, were relatively high due to a reduction in moisture content from brine soaking and cooking. The calcium level was high as expected because of the presence of bone, and sodium was elevated by the brine treatment.

Table 11.—Proximate composition of bone-softened shortbelly rockfish and jack mackerel. The fish were dressed, and cooked in an autoclave at 121°C and 15 p.s.i. for 40 minutes. Results are expressed in percent of dressed weight, or as otherwise indicated.

Item	Shortbelly rockfish	Jack mackerel
Moisture (%)	71.09	70.46
Total protein (%)	22.45	25.71
Fat (ether extract, %)	4.54	2.35
Ash (%)	1.67	1.65
Calories/100 g	132.00	124.00
Calcium (mg/100 g)	291.00	94.20
Sodium (mg/100 g)	136.00	239.00

Product Yield

The yields of bone-softened shortbelly rockfish and jack mackerel are given in Table 12. Shortbelly rockfish yield, 37.5 percent of the initial weight, was low compared to that for jack mackerel, 45.7 percent. Some of the weight loss for shortbelly rockfish is attributible to our processing and handling methods as considerable amounts of the soft cooked flesh fell apart and was lost during removal from the aluminum foil pouch. The moisture contents of both species are similar, averaging 76 and 75

Table 12.—Product yield for bone-softened shortbelly rockfish and jack mackerel. The fish were soaked overnight in brine solutions and cooked at 121°C and 15 p.s.i. for 40 minutes (shortbelly rockfish) or 30 minutes (jack mackerel).

Item	Shortbelly rockfish	Jack mackerel
Avg. total length	208 mm (8.2 in.)	250 mm (9.8 in.)
Avg. total wt.	88 g (3.1 oz.)	164 g (5.8 oz.)
Avg. dressed length	111 mm (4.4 in.)	
Avg. dressed wt.	48 g (1.7 oz.)	99 g (3.5 oz.)
Avg. wt. after cooking	33 g (1.2 oz.)	75 g (2.6 oz.)
Yield: Weight of cooked fish as percent of total wt.	37.5%	45.7%

percent for shortbelly rockfish and jack mackerel, respectively[3].

Outside Evaluation

The following procedure was followed to provide samples of bone-softened fish for outside evaluation.

Shortbelly Rockfish Samples

Fish were obtained directly from a fisherman and kept on ice for 2 days prior to processing. Fish averaging 88 g total weight were headed and gutted and washed. Half of the fish were then soaked in a 1.5 percent salt solution overnight at 5°C. One liter of this solution was used for 1.2 kg of dressed fish. The cured fish were aligned and wrapped in aluminum foil, and cooked in an autoclave at 121°C and 15 p.s.i. for 40 minutes. The uncured fish were also cooked in the same manner. All samples were then drained, and frozen individually at −25°C (−13°F).

Jack Mackerel Samples

Fish were obtained from a wholesale fish company, so no details of catch or handling were available. They were processed shortly after purchase. Fish averaging 164 g total weight were headed and gutted and washed, then soaked in chilled 2 percent salt solution, with the addition of 0.25 percent sodium polyphosphate. Tea extract at a concentration of 0.25 percent was included in the soaking solution. The extract was prepared by steeping 2.5 g of crushed green tea leaves per liter of water at 100°C for 40 minutes. One liter of soaking solution was used for each 900 g of fish. The cured fish were aligned and wrapped in aluminum foil and cooked at 121°C and 15 p.s.i. for 30 minutes. The fish were then drained and frozen individually at −25°C.

Table 13.—Sensory evaluation of bone-softened shortbelly rockfish and jack mackerel. This table was provided by Harold Barnett, Utilization Research Division, Northwest and Alaska Fisheries Center, NMFS, Seattle, Wash.

Sample	Odor[1]	Flavor	Texture	Acceptability	Rancidity[2]
Rockfish (control)	4.8 ± 1.7[3] (4)	4.5 ± 1.8 (6)	4.8 ± 1.6 (4)	4.5 ± 1.5 (4)	3.0 ± 2.1 (5)
Rockfish (soaked)	5.6 ± 1.4 (4)	4.9 ± 1.4 (4)	4.8 ± 1.6 (4)	4.9 ± 1.4 (4)	2.8 ± 2.3 (7)
Mackerel (soaked)	3.5 ± 2.1 (6)	4.1 ± 2.3 (6)	4.7 ± 2.2 (6)	3.4 ± 2.0 (6)	5.1 ± 2.6 (7)

[1] Sensory scale (except for rancidity) 9 to 1, with 9 indicating excellent and 1 poor quality. A score of 3 indicates a product of unacceptable quality.

[2] Rancidity scale 1 to 9, with 1 indicating no rancidity, 5 slight and 9 strong rancidity.

[3] Each number represents the mean of seven or eight evaluations ± the standard deviation. Numbers in parentheses represent differences between the highest and lowest scores.

Samples of bone-softened shortbelly rockfish and jack mackerel were shipped to the Utilization Research Division of the NMFS Northwest Alaska Fisheries Center, in Seattle. Before evaluation by a taste panel the samples were further treated by twice being dipped in batter and breaded. They were then deep-fried in vegetable oil from the frozen state at 190°C (375°F). Time required for cooking ranged from about 4 minutes for shortbelly rockfish to 7 minutes for jack mackerel. The cooked fish were served warm to an 8-member taste panel. The evaluation by the panel is summarized in Table 13.

Generally, individual panelists' reactions to both species were highly varied, but the average scores of both indicated a low to medium acceptance level. Shortbelly rockfish was judged to be better than jack mackerel in all respects, but this may have been due to high variability in the quality of the mackerel samples, some pieces of which were so rancid that one panelist declined to eat the product[4]. Shortbelly rockfish soaked in brine was preferred in all respects over those that were not soaked. Two panelists gave scores of 7 (= "good") in all of the sensory evaluation categories to soaked shortbelly rockfish. No hard bones were detected in either species by the panelists.

Discussion

Evidently many species of fish are amenable to a bone softening process. Among the groundfish and small pelagic species we tested, only the plainfin midshipman proved to have bones so hard as to be unsuited for the process. A secondary problem, emanation of objectionable odors, results from treatment at high temperatures. The odor, which is most pronounced in mackerels and sardines, probably needs to be reduced to increase acceptance of these species as bone-softened products.

The pelagic species have relatively large proportions of dark muscle, which contains higher levels of trimethylamine oxide (TMAO) as well as iron, than light muscle (Tokunaga, 1970). TMAO is broken down through cooking or bacterial action to trimethylamine (TMA), which is the source of most "fishy" odor (Tokunaga, 1975). Iron is a catalyst of thermal decomposition of TMAO to TMA. In Japan, green tea extract is commonly used to reduce this odor. The effective agents are the catechins, substances found in tea, which react with trimethylamine (Hata et al., 1980). Formation of disagreeable odors can also be decreased by using minimum times and temperatures when cooking fish in the autoclave. Thus, it is possible to manufacture satisfactory bone-softened products even with pelagic species which characteristically contain higher levels of TMAO.

In bone, insoluble calcium salts are supported by proteins and mucoids (nitrogen compounds), and the greater the calcium content, the harder the bone (Otani and Fujikawa, 1937). Bone softening by cooking is supposedly related to thermal decomposition of collagen, the main proteinacious component of bone, thus loosening the supporting texture. We expected that the minimum temperature necessary for softening bones of various species of fish might be correlated with the amount of calcium and collagen (or other nitrogen compounds) in the bone, but found no such relationship (Table 5). In fact of 11 species we studied, only the bones of the plainfin midshipman, and a rather large yellowfin tuna could not be easily softened, so this technique could be applied with many fishes.

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[3] Guide to underutilized species of California. Admin. Rep. T-83-01 (unpubl.) avail. at Tiburon Laboratory, Southwest Fisheries Center, 3150 Paradise Drive, Tiburon, CA 94920.

[4] Harold Barnett, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112. Personal commun.

In California, jack mackerel and Pacific mackerel are used mainly in canned form, for human consumption as well as cat food. A fair amount is also frozen for bait, and a small amount is sold as fresh fish. The average annual catch of these two species is high, compared with other California marine resources, amounting to over 50,000 tons annually. Thus these fish are good candidates for bone softening. Jack mackerel may be better suited for this process because it has firmer flesh with less red meat, however.

We find it particularly heartening that shortbelly rockfish makes an acceptable product, since this species is one of the most plentiful unused marine resources found off California. Although recent assessments of populations of shortbelly rockfish are not available, earlier works indicate that this species is abundant and easily caught in large numbers (Lenarz, 1980; Kato, 1981). Direct consumption of this fish is difficult because of the abundance of small bones and spines, and filleting is impractical because of the cost. Also, each fillet from mature individuals weighs only around 30 g (1 ounce), which is too small for most traditional methods of preparing rockfish.

Small, bony fish are not only inconvenient to eat, but their sharp bones and spines are also hazardous, especially to young children. Removing such bones before marketing is usually too costly, so most small fishes are not consumed directly. The introduction of bone-softening techniques around 1980 in Japan immediately made it possible to use a variety of small fishes and greatly increased the potential market for them. Because of its abundance, the Japanese sardine is the fish most used to make bone-softened products. A ready-to-fry breaded product is the most popular item. The bone-softening method used in Japan is essentially the same as that described here, but fish with coatings of various flavors are marketed, including curry, cream and parsley, and tomato. In addition, uncoated bone-softened fish are also sold. These are used directly in salads or other dishes applicable to canned tuna, or coated by the cook and fried. The composition of a breaded sardine product, with sesame seeds added for flavoring, is given in Table 14. Breaded fish are graded and packed in uniform size groups, around 25, 30, or 40 g per fish. At present, bone-softened fish is sold directly to institutional users only, and not in retail stores. The wholesale price in Japan for this product is about 25 yen per 25 g fish, or 1,000 yen/kg ($3.50/pound, at an exchange rate of 130 yen=$1.00). The price seems rather high when converted to U.S. dollars, but this is due to recent weakening of the dollar.

Table 14.—Proximate composition of Japanese commercial bone-softened breaded product made with sardine, *Sardinops melanostictus*, and percent composition of ingredients used to make the product. The data were provided by the manufacturer, Suzuhiro Co., Ltd., 245 Kazamatsuri, Odawara City, Kanagawa Prefecture, Japan.

Proximate composition of breaded product		Percent composition of ingredients	
Item	Comp	Item	Comp.
Protein	17.6%	Bone-softened sardine	63%
Fat	8.2%	Breading	20%
Carbohydrate	9.0%	Wheat flour	5%
Ash	0.6%	Salt	1%
Calcium	338 mg/100 g	Sesame seeds	5%
Salt	700 mg/100 g		
Calories	183 KCal/100 g		

To learn how U.S. consumers might react to bone-softened fish products, we obtained from Japan samples of bone-softened and breaded sardine, *Sardinops melanostictus*, and filefish, *Thamnaconus modestus*. The samples were deep-fried in vegetable oil and presented to several staff members of the Tiburon Laboratory of NMFS. Nearly everyone who tasted the samples thought that the filefish, a mild, white-fleshed fish, was good in taste and texture when deep-fried. The other sardine, however, was thought to be too "fishy." The bones of both species were undetectable to all tasters.

Samples of filefish were next given to about 400 persons, most of whom were connected with the fishing industry. One sampling was conducted at a seafood and wine tasting event held at the Olde Port Inn, in Avila Beach, Calif., in February 1987. A second informal tasting was also done in February in Sacramento, Calif., in conjunction with the "Fishermen's Forum," which is conducted annually by state legislators. Most comments received from tasters were favorable, and the use of small fish, with bones intact, was thought to be an excellent idea both from the standpoint of fish utilization, as well as health aspects because of high calcium content. Most tasters also liked the flavor and texture of the product. Negative comments related mainly to the addition of calories by frying in oil. Practically no tasters were able to detect the presence of the softened bones and spines.

Recommendations

To knowledgably start commercial production of bone-softened products in the United States, several questions still need to be answered. The most important is to learn whether American consumers would purchase such products, and how much they would be willing to pay. We also need to learn which species are acceptable, and if costs associated with processing of those species allow commercial production. Research is also needed on ways to maintain quality of frozen bone-softened products and, especially, to lower or slow the onset of rancidity.

Should market studies be contemplated, we feel that satisfactory sample products can be made by using the procedures outlined in Figure 1. Types of coatings applied to bone-softened fish is a different area of research, but we feel that plain batter and breading is sufficient to allow representative test marketing of the product. Another way to obtain samples for test marketing may be to have a Japanese firm already manufacturing bone-softened products provide market samples made from

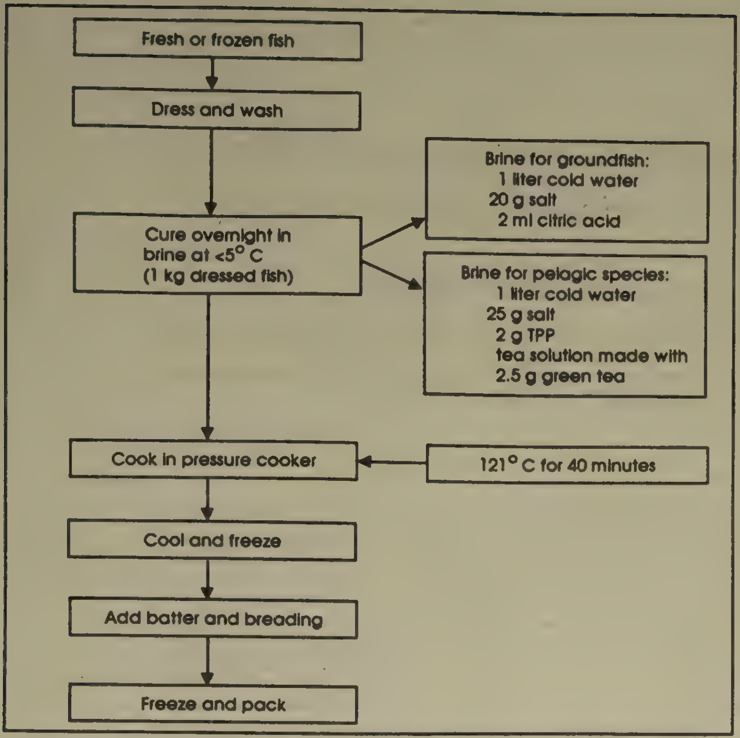
Fresh or frozen fish
Dress and wash
Cure overnight in brine at <5° C (1 kg dressed fish)
Brine for groundfish: 1 liter cold water 20 g salt 2 ml citric acid
Brine for pelagic species: 1 liter cold water 25 g salt 2 g TPP tea solution made with 2.5 g green tea
Cook in pressure cooker
121° C for 40 minutes
Cool and freeze
Add batter and breading
Freeze and pack

Figure 1.—Recommended procedures for making bone-softened groundfish and small pelagic species.

shortbelly rockfish and jack mackerel or other species with good potential (i.e., a large biomass). Processing costs may also be derived through such an arrangement.

Market research is needed to see if products other than deep-fried bone-softened fish are acceptable to the American consumer, who is becoming more and more conscious of calorie intake. Notwithstanding the questions remaining, we feel that bone softening is an effective means of utilizing species of fish that are too small for use in traditional forms, and we hope that this study will lead the way to eventual acceptance of this product form in the United States.

Acknowledgments

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Nearshore ichthyoplankton associated with seagrass beds in the lower Chesapeake Bay

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ABSTRACT: Estuaries serve as important nursery habitats for larvae and juveniles of many species of fishes and invertebrates. Within the estuary, however, partitioning may occur among main channel, mud flat, tidal creek, and vegetated habitats. In this study we describe the egg, larval, and juvenile fish assemblages in shallow areas of submerged aquatic vegetation (SAV) of the lower Chesapeake Bay and compare them with those over the adjacent, shallow sand habitat. Densities at night over all habitats were about 1 order of magnitude higher than daytime densities, and were highest in summer. The SAV habitats were not important spawning sites for species with pelagic eggs, but were important for species brooding eggs or with demersal eggs. Overall, collections were dominated by the bay anchovy *Anchoa mitchilli*, but contained many species not commonly found in the midchannel ichthyoplankton described in earlier studies; these include the croaker *Micropogonias undulatus*, rough silverside *Membras martinica* and northern pipefish *Syngnathus fuscus*. Conversely, the weakfish *Cynoscion regalis* was rare in our collections as compared to main channel sampling areas. Our results suggest that SAV areas do not play an important nursery role for pelagic eggs and early larvae, which may suffer increased predation by planktivores in these areas. Later stages, however, may benefit from reduced predation pressure from piscivores and thus benefit from association with SAV.

INTRODUCTION

The shallow, vegetated areas of estuaries serve an important role as nursery habitats for early life history stages of fishes and shrimps (Reid 1954, Carr & Adams 1973, Adams 1976, Orth & Heck 1980, Weinstein & Brooks 1983). The most frequently cited benefits of estuarine residence include enhanced prey availability (Houde & Lovdal 1984), and especially reduced predation (Rosenberg 1982, Bell et al. 1987). Predation may be reduced through increased turbidity in estuaries (Blaber & Blaber 1980, Boehlert & Morgan 1985) or through use of more structurally complex shallow-water areas not readily accessible to predators. Habitat complexity is increased by the presence of seagrass, and this apparently plays an added role in reduction of predation (Lascara 1981, Savino & Stein 1982, Minello & Zimmerman 1983, Heck & Thoman 1984). Although the juvenile and adult fishes in these seagrass beds have been surveyed (Orth & Heck 1980), relatively little is known about the importance of this habitat for fish eggs and larvae.

Within the lower Chesapeake Bay, late larval and juvenile fishes occupying seagrass habitats either immigrate from offshore spawning grounds or result from local spawning activity. In the former case, earliest development occurs in offshore waters and movement to the nearshore waters near inlets may be mediated by Ekman transport (Miller et al. 1984). Subsequent movement through inlets and habitat selection within estuaries is thought to depend upon behavioral mechanisms (Boehlert & Mundy 1988). Data on spawning activity of resident species are available from previous characterizations of Chesapeake Bay ichthyplankton (Pearson 1941, Dovel 1971, Olney 1983). These studies have concentrated on midchannel portions of the estuary and have neglected the generally inaccessible nearshore, shallow environments. As a result, the extent to which nearshore vegetated zones serve as spawning habitats for resident Chesapeake Bay fishes, particularly those with pelagic eggs, is unknown. Some resident species, especially those that brood eggs or have demersal eggs, are known to spawn in these nearshore habitats. For species with pelagic eggs, how-

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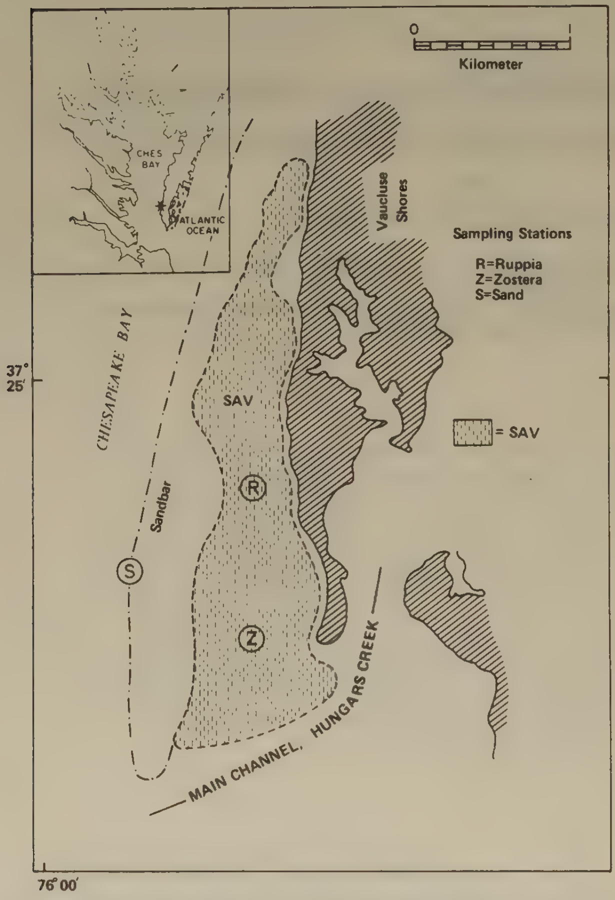

Fig. 1. Detail of sampling site at Vaucluse Shores, Virginia, USA. Inset locates study site (★) in Chesapeake Bay region. Pushnet samples were taken in *Zostera* (Z), *Ruppia* (R), and Sand (S)

ever, it is likely that tidal flushing or predation by resident planktivores would remove such eggs from the area.

In the Chesapeake Bay, areas of seagrass beds have declined (Orth & Moore 1983), possibly resulting in decreasing availability of nursery habitat. In the present study, we characterize nearshore ichthyoplankton associated with beds of *Zostera marina* and *Ruppia maritima* and examine spatial and temporal trends in recruitment of larval and early juvenile fishes to these shallow-water habitats. Finally, we evaluate the use of vegetated zones as spawning sites for resident Chesapeake Bay fishes.

MATERIALS AND METHODS

The sampling site was located on the eastern side of Chesapeake Bay, Virginia, USA (ca 37° 25′ N, 75° 59′ W) in an area known locally as Vaucluse Shores (Fig. 1). Three sampling stations, designated as *Zostera*, *Ruppia*, and Sand, were established within the nearshore system. Sampling depths typically ranged from 1.5 to 3 m. To avoid disturbance to the seagrass and bottom in these shallow waters, we used a bow-mounted pushnet (Fig. 2) similar to that described by Miller (1973) deployed from a 5.8 m outboard skiff. The pushnet was equipped with a 1 m, 505 µm mesh and two 18.5 cm, 202 µm mesh plankton nets fitted with calibrated General Oceanics* flowmeters. Nets were fished at night during slack high tide for 2 to 3 min depending on abundance of plankton. The sampling duration and boat speed allowed the ichthyoplankton net to cover 74 to 175 m^2 of sea surface and filter from 68 to 117 m^3 of water. Two replicate collections from each station were made monthly and preserved in 5 to 10 % laboratory grade formaldehyde in seawater buffered with sodium borate. In the laboratory, fish eggs and larvae were sorted from whole collections and identified to the lowest possible taxon. Larval lengths were measured with an ocular micrometer to the nearest 0.1 mm. Densities were calculated in volumetric and areal terms.

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* Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

RESULTS

General composition

The pushnet gear was effective for the collection of larval fish and zooplankton, as has been shown in other studies (Miller 1973, Hillman-Kitalong & Birkeland 1987); for studies in shallow water it is particularly effective in minimizing turbulence from the vessel and propeller which can result in suspension of sediment and benthos. One drawback, however, is the effective sampling depth. Although our samples were all taken in shallow water, station depths over sand were often slightly deeper (0.5 to 1.5 m) than in vegetated areas. Thus a smaller proportion of the water column may have been sampled over the sand habitat.

Pushnet sampling for ichthyoplankton resulted in 88 total collections (*Zostera*, $n = 31$; *Ruppia*, $n = 29$; Sand, $n = 28$) on 14 dates from 26 March 1979 to 7 March 1980. Volumetric and areal estimates of sampling effort revealed moderate monthly variability and almost equal sampling effort among habitats. Sampling was conducted at least monthly through January 1980, but inclement weather in February 1980 delayed completion of the survey until 6 March 1980. Day-night comparison sampling was conducted on successive high tides during May and August 1979.

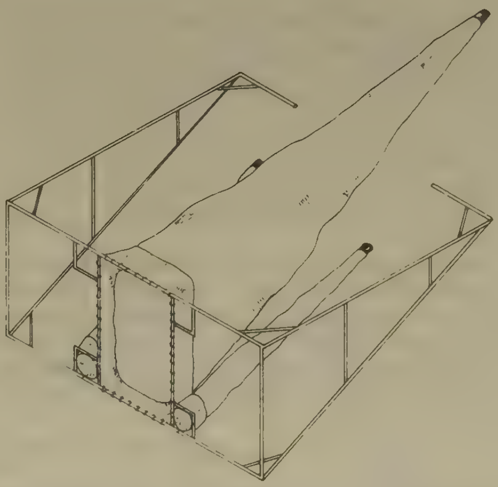

Fig. 2. Design of the pushnet sampling gear used to collect ichthyoplankton in the shallow-water areas; this design used a 1 m ichthyoplankton net and two 18.5 cm plankton nets. The 2 prongs were inserted into corresponding holes in the boat hull; the gear was carried in the boat and when deployed was swung forward and lowered over the bow of the boat. When the net was in use the top pipe was at the surface of the water

Temporal variability in hydrographic measurements was typical of shallow, nearshore environments, which are rapidly affected by short-term climatic changes (Fig. 3). Salinity, temperature, and dissolved oxygen samples were taken from the upper meter of the water column during sampling times; observed values (14.1 to 21.5 ‰; 1.5 to 28.0 °C; 6.6 to 12.6 mg l^{-1}, respec-

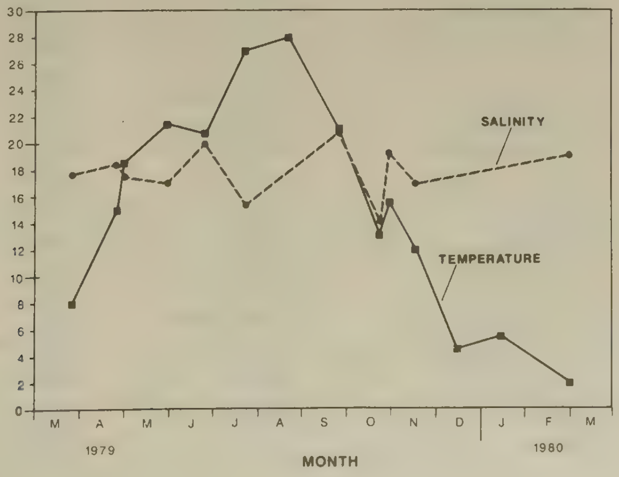

Fig. 3. Temperature and salinity measurements during the course of the study. These data are from the *Zostera* area during night sampling periods when ichthyoplankton samples were taken. Typically, there was little difference between the 3 areas at night

tively) were similar to those recorded by Orth & Heck (1980). Occasionally, temperature and salinity varied widely between successive sampling periods as evidenced by measurements recorded on 27 September and 1 November 1979 (Fig. 3). Throughout the 12 mo period, hydrographic values did not vary markedly among habitats during any given sampling period. As a result, they were not considered important factors in comparisons of ichthyoplankton abundances among habitats.

Pushnet collections yielded 24354 fishes and 8631 eggs representing 34 species in 20 families (Table 1). Fish eggs were present during the 6 mo period March to August 1979 (Fig. 4A). Eggs of 6 species of fishes were identified in pushnet collections, and eggs of unidentified species of the families Gobiidae and Sciaenidae were also captured; numerical dominants were *Anchoa mitchilli* (60.6 %), the Sciaenidae (35.7 %) and *Scopthalmus aquosus* (2.0 %). Mean densities of pelagic eggs of *A. mitchilli* and the Sciaenidae were higher over sand bottom than over either vegetated zone (Fig. 4A). Although eggs of the hogchoker *Trinectes maculatus* are typically conspicuous components of lower Chesapeake Bay ichthyoplankton (Olney 1983), eggs were taken in very low abundance and only over sand habitats. Eggs of the halfbeak *Hyporhamphus unifasciatus*, the rough silverside *Membras martinica*, and gobies (Gobiidae) were taken in low densities, generally attached to floating *Zostera* blades or other plant material over vegetated habitats.

Of the 33 species occurring as larvae and juveniles, 8 species made up 96 % of the total catch. A single

Table 1. Species, common name, life history stage and months of occurrence of fishes in pushnet collections, March 1979 to March 1980

Species	Common name	Stage	M	A	M	J	J	A	S	O	N	D	J	M
Anguilla rostrata	American eel	Elver	X											
Alosa aestivalis	Blueback herring	Juvenile	X	X								X		
Alosa pseudoharengus	Alewife	Juvenile					X							
Brevoortia tyrannus	Atlantic menhaden	Larva-juvenile	X	X	X	X					X	X	X	X
Anchoa mitchilli	Bay anchovy	Egg-adult	X	X	X	X	X	X	X	X	X	X	X	X
Anchoa hepsetus	Striped anchovy	Larva-juvenile					X	X						
Gobiesox strumosus	Skilletfish	Larva			X									
Hyporhamphus sp.	Halfbeak	Egg-juvenile			X	X	X	X						
Membras martinica	Rough silverside	Egg-adult		X	X	X	X	X	X	X				
Menidia menidia	Atlantic silverside	Adult	X	X		X						X	X	X
Atherinidae	Silversides	Larvae		X	X	X	X	X	X					
Gasterosteus aculeatus	Threespine stickleback	Juvenile		X										
Hippocampus erectus	Lined seahorse	Young					X							
Syngnathus fuscus	Northern pipefish	Larva-adult			X	X	X	X	X	X				
Cynoscion regalis	Weakfish	Larva-juvenile			X	X	X	X						
Sciaenops ocellatus	Red drum	Larva						X						
Menticirrhus americanus	Southern kingfish	Larva						X						
Leiostomus xanthurus	Spot	Larva-juvenile		X	X		X							X
Micropogonias undulatus	Atlantic croaker	Larva						X	X		X	X	X	
Bairdiella chrysoura	Silver perch	Larva						X						
Sciaenidae	Drums	Egg			X	X	X	X						
Tautoga onitis	Tautog	Egg		X										
Astroscopus guttatus	Stargazer	Larva					X							
Hypsoblennius hentzi	Feather blenny	Larva			X	X	X	X		X				
Chasmodes bosquianus	Striped blenny	Larva					X							
Ammodytes americanus	Sand lance	Larva												X
Gobiosoma ginsburgi	Seaboard goby	Larva						X	X			X		
Gobiosoma bosci	Naked goby	Larva								X				
Gobiosoma sp.	Gobies	Egg-larva			X	X	X	X						
Microgobius thalassinus	Green goby	Larva				X	X	X						
Gobionellus hastatus	Sharptail goby	Larva								X				
Peprilus paru	Harvestfish	Larva						X						
Paralichthys dentatus	Summer flounder	Larva	X	X							X	X	X	X
Scopthalmus aquosus	Windowpane	Egg-Larva	X	X	X									
Pseudopleuronectes americanus	Winter flounder	Larva	X											
Trinectes maculatus	Hogchoker	Egg-Larva				X		X						
Symphurus plagiusa	Blackcheek tonguefish	Larvae						X						
Sphoeroides maculatus	Northern puffer	Larvae						X						
Unknown	–	Eggs		X	X									

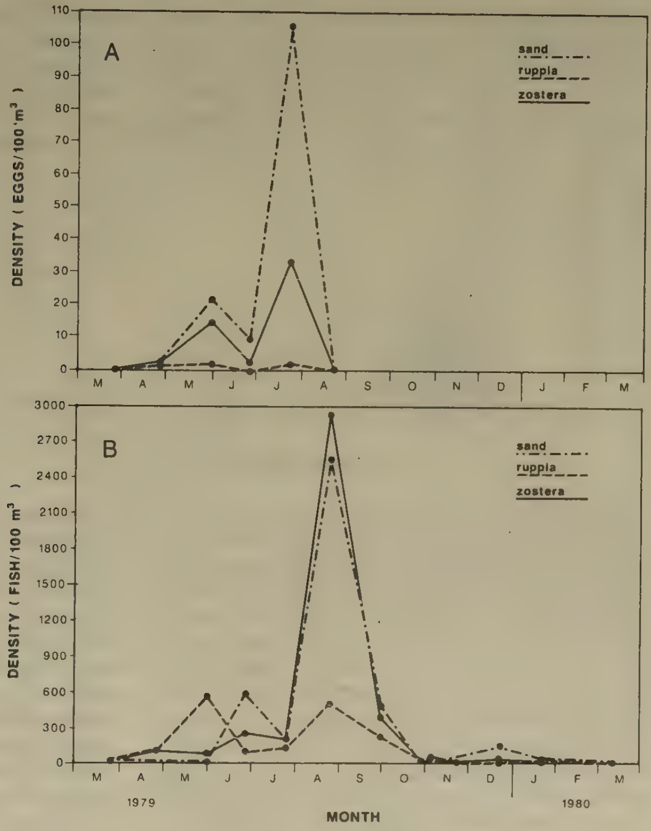

Fig. 4. Seasonality of the abundance of total fish eggs and larvae by habitat (*Zostera*, *Ruppia*, or Sand) throughout the course of the study. Values are the mean of duplicate samples. (A) Fish eggs. (B) Fish larvae

species, *Anchoa mitchilli*, dominated collections, comprising 72 % of all fishes captured. The remaining 7 species in order of decreasing abundance were the goby *Gobiosoma* sp. (8.9 %), juvenile menhaden *Brevoortia tyrannus* (6.06 %), larval through adult northern pipefish *Syngnathus fuscus* (3.9 %), larval and early juvenile croaker *Micropogonias undulatus* (2.2 %), juvenile and adult rough silverside *Membras martinica* (1.3 %), larval and early juvenile spot *Leiostomus xanthurus* (1.2 %), and unidentified atherinid larvae (1.1 %). Larval or juvenile stages were present during all months sampled (Fig. 4B). Mean abundance of fishes in all habitats gradually increased throughout the spring to a midsummer peak, generally reflecting maximum densities of larval anchovies.

We compared day and night pushnet catches in May

Table 2. Day versus night pushnet catch (numbers 100 m^{-3}) comparison, August 1979. Pelagic egg abundance estimates are excluded. Totals for all species at night include densities of several species not captured in day samples. Abbreviations are: S, sand; R, *Ruppia maritima*; Z, *Zostera marina*; T, total fishes captured in all habitats divided by total water volume filtered

Species	Day				Night			
	S	R	Z	T	S	R	Z	T
Anchoa mitchilli	97.2	2.9	46.4	54.7	2378.8	283.0	2648.8	1838.3
Atherinid larvae	2.8	3.9	1.0	2.6	1.5	46.9	14.3	19.4
Syngnataus fuscus	1.2	0.6	0.5	0.8	10.0	39.2	10.1	48.8
Gobiosoma sp.	0	0	0.5	0.2	65.9	74.8	150.2	96.7
All species	101.2	7.4	48.5	58.2	2513.1	474.1	2978.4	2055.2

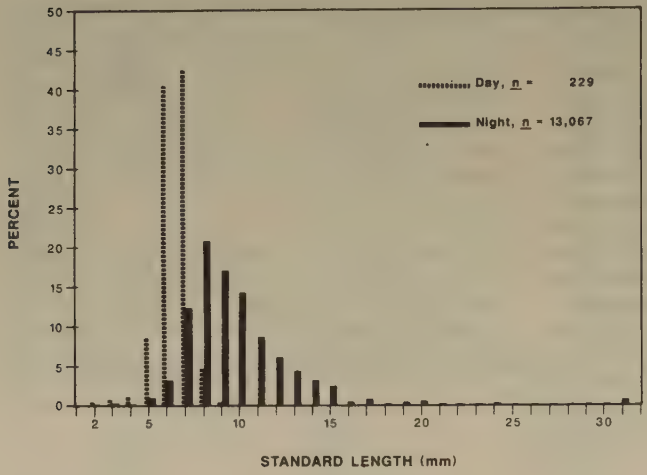

Fig. 5. *Anchoa mitchilli*. Day-night difference in the length frequency of larvae captured by pushnet in August 1979

and August. In both months, mean density estimates for all species in each habitat as well as total fishes captured in all habitats were much greater at night. In August 1979, when larvae were more abundant (Fig. 4B), 17 species of fish were captured at night, but only 4 species were taken in day collections (Table 2). Bay anchovies dominated collections, with density estimates of larvae in night collections significantly exceeding those in daylight collections. In addition, size-frequency analysis of day- versus night-caught larvae revealed extreme disparity in larval size distribution (Fig. 5). Anchovies larger than 9.0 mm SL were not taken during daylight hours but were a significant component of the night anchovy catch. These large specimens were either migrating to the upper meter from a deeper daytime distribution (Hunter & Sanchez 1976) or were not captured during daylight hours due to gear avoidance. It should be pointed out that the smallest sizes of newly hatched *Anchoa mitchilli* (2 to 4 mm SL) may be under-represented in our collections due to extrusion through the meshes (Houde & Lovdal 1984). This may also apply to small sciaenids. In comparisons between the remaining 3 species, size ranges did not differ markedly, but density estimates of silverside, goby, and pipefish larvae were greater in night collections. Because day densities represent a small percentage of night densities, daylight samples were not considered further in our analysis.

The bay anchovy *Anchoa mitchilli* was clearly the dominant species throughout our study. Peak monthly densities of bay anchovies were recorded in all habitats in June to September 1979, a 4 mo period that includes the time of peak spawning (Olney 1983) and during which larval and early juvenile stages dominated collections (Fig. 6A). Bay anchovies were present in pushnet samples during all sampling periods and in all habitats during each sampling period with the exception of March 1979 *Ruppia* collections. In general, monthly mean densities of bay anchovies varied only slightly between habitats, with the exception of August 1979. During this period of peak abundance, larval anchovies were conspicuously less abundant over *Ruppia* beds. Numerically, pushnet catches over *Ruppia* contributed only 9.6 % of the total anchovies taken during the study, while densities of anchovies over sand and *Zostera* beds appeared to be habitat-independent. The length-frequency distributions of bay anchovies show growth of the cohort between July and October. Based upon median sizes in the dominant mode of smaller larvae in July through October, the growth rate estimates were 0.13 mm d^{-1} (July–August), 0.29 mm d^{-1} (August–September), and 0.79 mm d^{-1} (September–October). Continued recruitment of newly hatched fish in August makes the first estimate low, but the second two are probably good estimates of field growth rate for this species. The mean of these 2 values, 0.54 mm d^{-1}, agrees well with observations of growth rates in the laboratory (Houde 1974, Houde & Schekter 1981) and field (Leak & Houde 1987).

Catches were dominated by juvenile and adult anchovies (fishes >30 mm SL) in March to May 1979 and October to December 1979. Larval anchovies appeared in collections in May 1979, corresponding to the time of first occurrence of pelagic eggs (Fig. 4A). By September 1979, spawning had apparently ceased and no early larval stages appeared in collections. Young anchovies ranged from 10 to 32 mm SL and this larval cohort dominated September catches. Late larval and early juvenile stages (16 to 30 mm SL) remained in pushnet collections throughout the remainder of sampling (October 1979 to March 1980), apparently a period of minimal growth. The presence of specimens smaller than 30 mm SL taken in November, however, suggests that a minor late spawning may have occurred after that in the May to August period. The occurrence of these small fish, however, was sporadic; they seemed absent in December but were present again in March 1980. The presence of 30 to 50 mm SL fish in May through June 1979 suggests that this late spawning occurred in 1978 as well.

Different species groups showed clear temporal patterns (Table 3). Seasonality of pushnet-collected

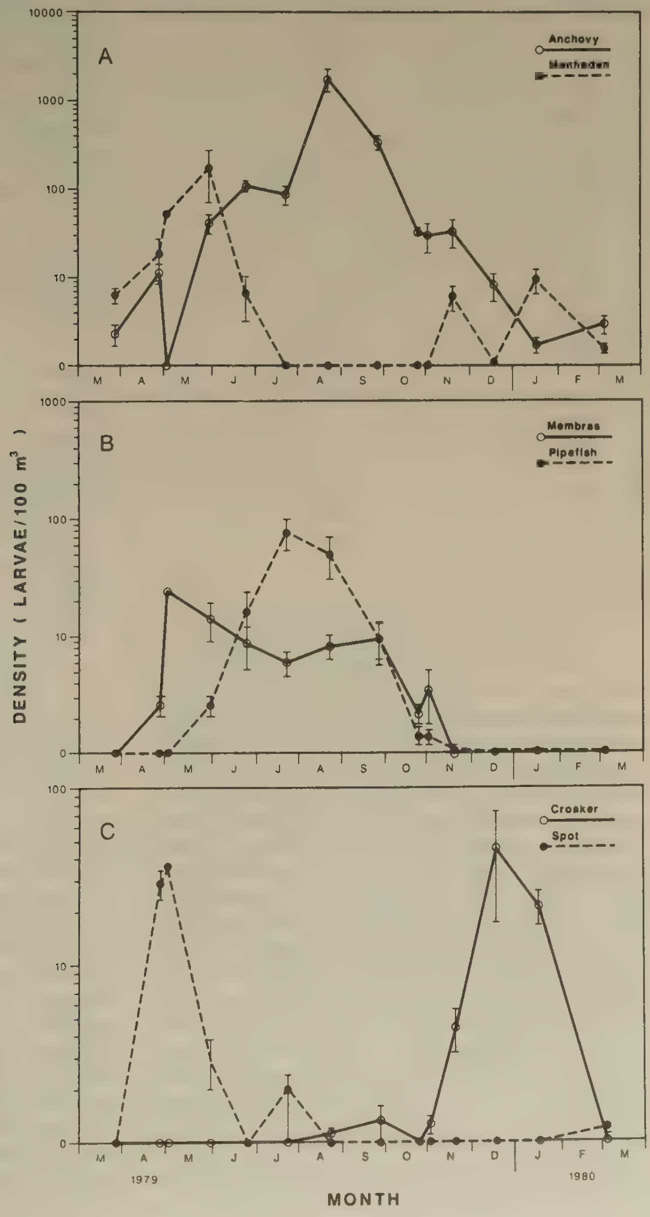

Fig. 6. Seasonal abundance of larvae of the principal taxa from all 3 habitats combined. Values are means of all observations, with bars representing ±1 SE. (A) Bay anchovy *Anchoa mitchilli* and Atlantic menhaden *Brevoortia tyrannus*. (B) Northern pipefish *Syngnathus fuscus* and rough silverside *Membras martinica*. (C) Spot *Leiostomus xanthurus* and Atlantic croaker *Micropogonias undulatus*

Table 3. Summary of seasonal ichthyoplankton assemblages in nearshore habitats in Chesapeake Bay. Species life history stages (E: egg; L: larva; J: juvenile; A: adult), surface temperature range and months of collection are reported from pushnet collections, March 1979 to March 1980

Surface temperature range (°C)	Season (months)	Characteristic species	Life history stages
1–12	Winter (Nov–Mar)	*Ammodytes americanus*	L
		Brevoortia tyrannus	L, J
		Paralichthys dentatus	L, J
		Anguilla rostrata	Elver
		Micropogonia undulatus	L
		Anchoa mitchilli	J, A
		Menidia menidia	J, A
15–22	Spring (Apr–May)	*Leiostomus xanthurus*	L, J
		B. tyrannus	L, J
		Membras martinica	J, A
		A. mitchilli	E, L, J, A
		Scopthalmus aquosus	E, L
		Atherinidae	L
		Syngnathus fuscus	A
		Sciaenidae	E
20–28	Summer (Jun–Aug)	*A. mitchilli*	E, L, J, A
		Gobiosoma sp.	L
		A. hepsetus	L
		S. fuscus	L
		Sciaenidae	E, L, J
		M. martinica	E, J, A
		Atherinidae	L
		Microgobius thalassinus	L
		Hyporhamphus sp.	E, L
		H. hentzi	L
13–21	Fall (Sep–Oct)	*A. mitchilli*	L, J, A
		Membras martinica	J, A
		S. fuscus	J, A
		H. hentzi	L, J

fishes was related to water temperature, with higher densities in warmer months (Figs. 3 and 4). Winter pushnet collections (November to March) were characterized by larvae or early juveniles of 5 species of offshore spawners, specifically *Ammodytes americanus, Brevoortia tyrannus* (Fig. 6A), *Paralichthys dentatus, Anguilla rostrata*, and *Micropogonias undulatus* (Fig. 6C). Larval stages of these fishes (elvers in the case of American eel) enter the Chesapeake Bay when surface water temperatures ranged from 1 to 12 °C. Patterns and mechanisms of immigration into the bay are unknown, but the presence of these stages in nearshore habitats along the eastern bay margin is probably related to Bay salinity patterns. The eastern bay margin is characterized by a high salinity salt wedge intrusion (Boicourt 1981). Late stage larvae may utilize the non-tidal, upriver vector of this intrusion as a mechanism in recruitment to the estuary. The absence of dense *Zostera* or *Ruppia* beds during the winter precludes utilization of SAV habitat. In addition to immigrant larvae, resident populations of juvenile and adult *Anchoa mitchilli* and *Menidia menidia* occupy nearshore waters during winter (Fig. 6).

With increasing surface temperatures (15 to 22 °C), spring pushnet collections revealed the continued presence of *Brevoortia tyrannus* larvae and juveniles as well as resident populations of juvenile and adult anchovies and rough silversides (Fig. 6). Larval and juvenile spot *Leiostomus xanthurus* became most abundant (Fig. 6C, Table 3). Resident populations of juvenile and adult anchovies and rough silversides were apparent (Fig. 6A, B). Spawning activity of bay anchovies, sciaenids, and windowpane flounder *Scopthalmus aquosus* were responsible for the increased egg densities during this period (Fig. 4A). Atherinid spawning and the presence of adult *Syngnathus fuscus* and young spot in collections coincide with the initiation of SAV growth.

The summer SAV ichthyoplankton assemblage was characterized by high densities (Fig. 4) and was dominated by egg and larval stages of resident lower Chesapeake Bay spawners including anchovies, gobies, pipefish (Fig. 6B), sciaenids *(Cynoscion regalis, Menticirrhus americanus, Sciaenops ocellatus,* and *Bairdiella chrysoura),* atherinids, blennies, and halfbeaks (Table 3). In addition, some immigration of offshore (or coastal) spawned larvae was observed, namely *Anchoa hepsetus.* Summer pushnet collections revealed peaks in density and diversity of nearshore ichthyoplankton populations but habitat comparison data (Fig. 4) confirmed that these peaks were independent of the presence of dense SAV beds. The high numerical rank abundance of goby and pipefish larvae, however, was clearly a function of water depth and the presence of vegetation. This conclusion is based on the relative importance of the species in ichthyoplankton surveys of deeper waters in the Bay (Pearson 1941, Olney 1983). Late stage larval, juvenile, and adults of 4 species, all resident lower Bay fishes, were present in fall (September, October) pushnet collections. During this period, density and diversity of the catch were low and little evidence of SAV dependence was observed (Fig. 4).

DISCUSSION

Studies of ichthyoplankton distribution have recently shown that many difficult-to-sample habitats may harbor significant populations of larval fishes. These include the epibenthic stratum (Jahn & Lavenberg 1986), the surf zone (Senta & Kinoshita 1985), near rocky reefs (Marliave 1986, Kobayashi 1987), shallow waters of estuaries (Powles et al. 1984), and seagrass beds, as shown in the present study. We noted moderate abundances of larvae which were either rare *(Micropogonius undulatus)* or unreported *(Anchoa hepsetus, Sciaenops ocellatus)* in previous studies in the Chesapeake Bay (Pearson 1941, Olney 1983). Conversely, species abundant in main channel areas, including *Cynoscion regalis* and *Trinectes maculatus,* were rare in our samples.

While our data demonstrate that nearshore vegetated habitats in lower Chesapeake Bay are not important spawning sites for species with pelagic eggs (Fig. 4A), they are clearly important for some species that either brood young (syngnathids) or have demersal eggs (atherinids). Certain other estuarine species with demersal eggs or nesting habitats, including gobies, blennies, or toadfish *Opsanus tau,* frequently occur within SAV habitats during spawning periods, but are probably not dependent upon these habitats. In our study the dominant species were either widely distributed across all habitats (bay anchovy, menhaden) or transients making short-term utilization of the seagrass habitat. Some of these species, such as spot, may in fact be more abundant in tidal creeks (Weinstein 1979) or other unvegetated areas (Heck & Thoman 1984). Weinstein & Brooks (1983) suggested that shallow tidal creeks may be the preferred habitat, and as these become saturated with young spot, the less preferred vegetated habitats are utilized. Thus, the importance of seagrass beds as spawning sites and as an early larval nursery habitat may be questioned.

Bell & Westoby (1986a) conducted experiments with artificially reduced seagrass densities and caged and uncaged treatments. Their results suggested that abundance of macrofauna in seagrass beds is a function of habitat preference rather than lower predation rates. Later, however, they attributed a selective advantage to species with early life history stages using the complex seagrass habitats to reduce predation (Bell & Westoby 1986b). This protection role may be questioned for early life history stages of fishes and the degree of protection may relate to the stage of ontogenetic development. It is clear that the complex habitat provided by seagrass may provide protection for animals able to orient to the blades under certain conditions (Heck & Thoman 1981, Minello & Zimmerman 1983). Breitburg (1987), for example, observed presettlement larval *Gobiosoma bosci* schooling within 0.5 m of the substrate in Chesapeake Bay. The same habitat complexity, however, often results in higher densities of animals which prey on early life history stages of fish and plankton in particular. In kelp forests, for example, fishes remove significant portions of the plankton flowing through (Bray 1980); Gaines & Roughgarden (1987) showed that predation by planktivorous fishes in nearshore kelp beds had a negative effect on recruitment of intertidal barnacles. Seasonally high abundances of planktivorous fishes such as silverside, spot, silver perch, pipefish, and other species (Orth & Heck 1980) may result in SAV beds serving as 'sinks' for pelagic eggs and early larvae, which are unable to orient to the seagrass blades. Leak & Houde (1987) observed predation related mortality of 18 to 28 % d^{-1} for *Anchoa mitchilli* larvae in Biscayne Bay, Florida, USA. In our study, the major difference in abundance between day and night pushnet samples (Fig. 5) for this species may be partially the result of predation, since planktivores typically feed during daylight hours (Ryer & Boehlert 1983). The ratios of night to day densities of bay anchovy larvae by habitat in August were 24.5, 97.6, and 57.2 for sand, *Ruppia,* and *Zostera* areas, respectively. The dramatically greater decrease in day densities in vegetated areas may thus be in part related to local abundance of predators.

As opposed to early larval stages, the refuge function of seagrass may be well served for late larvae and juveniles of some species, such as menhaden, spot, and silverside. The increased development of sensory systems and swimming capabilities in older larvae (Fukuhara 1987) may make them better able to evade many predators in seagrass. This would agree with suggestions that post-settlement mortality from predation is relatively unimportant (Bell et al. 1987). Lascara (1981) demonstrated through laboratory experiments that larger, predatory fishes such as bluefish or weakfish are less able to prey upon juvenile fishes with increasing seagrass density. Similar results were noted by Savino & Stein (1982), who further attributed these effects both to increases in visual barriers for predators and adaptive changes in behavior of the prey species; early larvae may be unable to exhibit such behavior patterns. A further benefit to late larval stages in estuarine environments may be lower densities (or reduced predatory capabilities) of gelatinous predators, which can have important impacts upon fish larvae (van der Veer 1985).

That estuaries serve as important nursery habitats for early life history stages of fishes has been clearly demonstrated (Weinstein et al. 1980, Boehlert & Mundy 1987). Our study shows that the nearshore and seagrass habitats in the Chesapeake Bay are characterized by many species which are not commonly found in the midchannel ichthyoplankton as described by Olney (1978, 1983) and others. A full characterization of ichthyoplankton communities requires examination of nearshore, nearbottom, and other difficult-to-sample habitats, many of which will require novel or new sampling methodologies.

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Annex I
Report of the Sub-Committee on Small Cetaceans

Members: Brownell (Convenor), Aguilar, Anderson, Arnason, Best, Bjorge, Bloch, Born, Buckland, Christensen, Collet, Desportes, Donovan, Gaskin, Gong, Hammond, Horwood, Jean-Caurant, Kasamatsu, Kasuya, Kato, Klinowska, Leatherwood, Lens, Lockyer, Lyrholm, Mae, Martin, Moore, Nerini, Ohsumi, Øien, Payne, Perrin, Reeves, Reilly, Shima, Smith and Wada.

1. ELECTION OF CHAIRMAN

Perrin was elected Chairman.

2. APPOINTMENT OF RAPPORTEURS

Reilly acted as rapporteur for the sessions of the sub-committee on pilot whales. Buckland, Collet, Klinowska, Reeves and Smith also served as rapporteurs.

3. ADOPTION OF AGENDA

The Agenda adopted is given in Appendix 1.

4. REVIEW OF AVAILABLE DOCUMENTS AND REPORTS

The sub-committee considered documents SC/39/SM1–25 and the national progress reports. Documents SC/39/O 1, 10, 13, 14 and 26 also contained information on small cetaceans.

5. REVIEW OF LIFE HISTORIES AND STATUS OF POPULATIONS OF PILOT WHALES, *GLOBICEPHALA* SPP

The genus *Globicephala* includes two species of small whales found throughout much of the tropical and temperate waters of the world. The sub-committee was pleased to receive the substantial amount of new information on North Atlantic *G. melaena*[1], with additional information available for Southern Hemisphere *G. melaena* and western Atlantic *G. macrorhynchus*.

5.1 Long-finned pilot whales, *G. melaena*, in the North Atlantic

5.1.1 Stock identity and distribution

There are no data available to distinguish pilot whales in the eastern North Atlantic from those in the western North Atlantic. However, this problem has not been systematically addressed. Electrophoretic data from a sample of 628 individuals from nine schools in Faroese waters (SC/39/SM13) indicated possible heterogeneity. Statistical analysis implied that the school captured in the northernmost location (Vidvik) of the nine might be different from the rest in this analysis.

The sub-committee concluded that more information on distribution, migration and genetics was needed to resolve issues of stock discreteness. Two studies planned for the coming year in the Faroes will hopefully provide some of this information: DNA-based studies now being conducted at Cambridge University and plans to satellite-tag three pilot whales and physically mark (freeze brand, fin notch and inject with tetracycline) as many others as possible from a single pod, reported by Martin.

5.1.2 Abundance

Information was presented in SC/39/SM14 for an offshore area of the North Atlantic resulting from four sighting surveys aimed at studying fin whales, conducted during 1981–4. This document presented preliminary estimates of pilot whale abundance based on 25 sightings. The authors noted that these results applied only to the area surveyed, which is probably only part of the range of the population involved. They also discussed some probable biases and mentioned that these results were probably minimum estimates.

The sub-committee expressed a number of reservations about the abundance estimates presented in SC/39/SM14. Because of the small number of sightings and the variability in school size, the standard errors of all the estimates of population size are approximately as large as the estimates themselves, so that 95% confidence intervals include zero in all cases. There were also problems noted with the fitting of a model to the perpendicular distance estimates. Although SC/39/SM14 provided a useful investigation of the available data and methods of analysis, these problems dictate that they cannot, without additional data, be used for a population estimate. The sub-committee also noted that *G. macrorhynchus* has been recorded from the southern part of the survey area.

The sub-committee believed that the school-size estimates were of particular interest, since they were made by experienced observers and were notably smaller on average (12–25) than those reported for this area by Duguy and Aloncle (1975) and for schools driven ashore in the Faroes (SC/39/SM23). Small schools have also been reported from the Mediterranean (McBrearty *et al.*, 1986).

SC/39/SM25 presented information from opportunistic sightings and strandings in British and Irish waters. The sub-committee agreed that, while there were some interesting and valuable data in this document, it was difficult to interpret opportunistic data without some measure of sighting effort. For example, in this document the increases indicated from both sightings and strandings in recent decades were far too large to reflect population increases and more likely reflect an increase in interest in cetaceans. However, they may reflect shifts in distribution or migration patterns. The seasonal data undoubtedly include effects of varying visibility conditions and other factors unrelated to actual pilot whale abundance.

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[1] *Editor's note*. Subsequent to the meeting, Perrin drew attention to the proposed change of *G. melaena* to *G. melas* (Jones, J.K. Jr, Carter, D.C., Genoways, H.H., Hoffman, R.S., Rice, D.W. and Jones, C. 1986. Revised checklist of North American mammals north of Mexico. *Occas. Pap. Mus. Texas Tech. Univ.* 107pp.).

Sightings of pilot whales made during aerial surveys of minke whales in coastal waters of Iceland were presented in SC/39/O 13. Records of pilot whales along the coast of France were summarised in SC/39/SM21; strandings there have been most frequent during the winter months.

5.1.3 *Migration*

No new data were presented which provided information on migration. SC/39/O 26 and Jean-Caurant *et al.* (1987) discuss levels of trace compounds in pilot whales (and other animals) from the Faroes. Appendix 3 discusses potential uses of such data in the study of home ranges and migrations.

5.1.4. *Life history*

5.1.4.1 *Age determination*

The sub-committee last year (*Rep. int. Whal. Commn* 38:123) concluded that the most important need concerning age-related parameters was that for standardisation of techniques used in age determination. Data in SC/39/SM16 indicate that the best technique involves counting of cemental growth layers in decalcified, sectioned and stained teeth. This method was also used by Kasuya and Matsui (1984) in studies of short-finned pilot whales from Japanese waters and by Kasuya *et al.* (SC/38/SM11) in a re-examination of data for long–finned pilot whales from Newfoundland waters.

The sub-committee believed these methods appeared most promising, but examination of resulting age-distributions left open the question of accuracy of the methods (see Item 5.1.4.2). The lengths at age calculated from these data were very close to those reported for the recent British strandings (Martin *et al.*, 1987).

5.1.4.2 *Age distributions*

Information on age distributions was provided in SC/39/SM16 and 20. Both indicated age distributions with 'missing' portions in the age interval from approximately 5 yrs to 15 or 20 yrs. Possible explanations for this are that reproductive or mortality rates have varied greatly (in which case the anomaly should progress with time), that there is segregation by age (with juvenile schools not available to the fishery) or that there is a systematic bias in the age determination method, (i.e. under-estimation of age in older animals).

5.1.4.3 *Sexual maturity*

A variety of estimates of age at sexual maturation of females was reported (6-8yrs: SC/39/SM21; 10yrs: SM15; 9yrs: SM16). The differences could be due to the relatively smaller sample size of the French coastal data set, or to slightly different methods used for age determinations. Kasuya *et al.* (SC/38/SM11) calculated six years as the female age at attainment of maturity for western North Atlantic pilot whales. Spermatogenesis begins at the age of five years but functional maturity is not attained before about 15 years of age (SC/39/SM21). Both SC/39/SM21 and SM15 estimated the length at maturity for males to be about 500cm. There appeared to be no standardisation of criteria for determining male sexual maturity in the reviewed papers.

5.1.4.4 *Reproductive rates*

SC/39/SM15 provided a number of estimates of reproductive parameters. Ovulation occurred at an average interval of 2.9 yrs. Conceptions and births were diffusely seasonal with a peak in conceptions from April to June and in births from July to October. Gestation is estimated to last 14.5 months (Sergeant, 1962).

Martin proposed in SC/39/SM15 a simple but novel procedure to estimate annual pregnancy rate. Using the estimate of foetal length at approximately 2.5 months at 12.5cm, he simply divided the number of females with foetuses over this length by the total number of mature females to arrive at an estimate of 0.28. Some members believed that the timing of the sample in relation to the peaks of conception and parturition could introduce bias. Others thought the method robust to this problem. No consensus was reached on the validity of this method. Possible biases notwithstanding, the resulting calving interval estimate of 3.5 yrs is closer to Sergeant's (1962) estimate of 3.3 yrs for Northwest Atlantic long-finned pilot whales. It is likely that the calving interval for individuals is a whole number of years. A gross reproductive rate of approximately 11% was estimated from the ratio of 46 females who would have given birth in the next 12 months to a total of 392 animals in the target pods. Martin and Desportes (SC/39/SM15) estimated lactation to last 27.3 months; 5 months longer than Sergeant's (1962) estimate. Twenty percent of the pregnant females were simultaneously lactating and pregnant. It was noted that this would change seasonally; the 20% estimate may not be accurate as an annual estimate.

5.1.5 *Exploitation*

There were no new analyses available to the sub-committee of the Faroes time series of catches. SC/39/SM2 presented preliminary results of a search for historical records of pilot whale catches in drive fisheries in the British and Irish Islands since the early 18th Century. Peak catches of up to several pods a year occurred in the mid 1800s. The last drive occured early in this century. Klinowska noted that the statistics are partial and that additional catch records probably reside in the files of regional museums and record repositories. The sub-committee noted the potential value of such data for analysis of long-term patterns in exploitation across the North Atlantic.

SC/39/ProgRep Denmark (Faroe Islands) reported that 1 of 19 bays previously authorised by the Faroes Government for use in the drive fishery has been closed and improvement of two beaches to increase the efficiency of the killing operation has been undertaken.

The fitness of the pilot whale meat for human consumption has implications for continued exploitation in the Faroes. As noted above, results of past studies of contamination by mercury and persistent organochlorines were presented in SC/39/O 26, and Jean-Caurant *et al.* (1987) summarised preliminary results of ongoing investigations of heavy-metal contamination. Mean levels of cadmium and mercury are relatively high in the population. The sub-committee recommended that these studies be continued and that a broad survey of organochlorines be initiated.

5.1.6 Status

No new information was available to the sub-committee that would allow assessment of status. The results of the planned cooperative international North Atlantic Survey may provide estimates of abundance that in conjunction with the results of research in progress on life history and composition of the catch will allow an attempt at assessment of status.

5.2 Other populations of *G. melaena*

Sightings of the long-finned pilot whale off southern South America were summarised in SC/39/SM4. The summary of cetacean sightings during the IDCR cruises, 1978/79 to 1983/84 (SC/39/O 10) also included sightings of the species in Antarctic waters and in the areas of the South Atlantic, South Pacific and Indian Oceans transited by the survey vessels *en route* to or from the Antarctic. The sub-committee noted a gap in the distribution of pooled sightings between approximately 45° and 50°S. The apparent hiatus may be an artifact of differential sighting effort or sighting conditions but should be investigated as a possible real gap in distribution. The sub-committee **recommended** that every opportunity be taken to collect sightings in these latitudes, with records or estimates of sighting effort.

Pilot whales were the eleventh most commonly recorded species (of thirteen) during the Antarctic surveys (SC/39/O 10). Pilot whales were scarce in waters of 0 – 5°C, where other species were common. Average school size was roughly comparable to those recorded for the North Atlantic populations (SC/39/SM20 and 23 and earlier references cited in SC/39/O 10). The sub-committee commended SC/39/O 10 as the results of the first attempt to systematically survey the small cetaceans of the Southern Ocean.

5.3 *Globicephala macrorhynchus*

Biological data gathered from mass strandings along the US East coast were presented in SC/39/SM22. The paper included estimates of age at attainment of physical maturity, but the sub-committee believes that these may not be correct, because of difficulties with age determination. Brownell reported that the authors plan to expand and complete analyses of the material and will make the results available to the sub-committee.

Records of pilot whales (of both species) in the Indian Ocean were presented in SC/39/SM4 (which had also been submitted to the Scientific Meeting on the Indian Ocean Sanctuary).

6. REVIEW OF NEW INFORMATION ON OTHER EXPLOITED SMALL CETACEANS

6.1 The dolphin/tuna problem in the Eastern Tropical Pacific

Three papers were presented with information on the status of populations of dolphins which are killed in the multinational tuna purse seine fishery. Two papers presented information on the dolphins killed. SC/39/SM12 presented numbers and species composition for 1986. SC/39/SM1 presented information from biological data and specimens collected from animals sampled from the kill. A third paper (SC/39/SM9) presented information on dolphin abundance over time developed from sightings data collected during the operation of the fishery. These three papers provided substantial new information that may not be consistent with previous assessments of the status of several of the dolphin populations affected by this fishery.

6.1.1 Estimates of mortality

SC/39/SM1 presented a breakdown of the incidental kill of six populations of five species, similar to previous reports (e.g. SC/38/SM1).

SC/39/SM12 presented estimates of the kills of dolphins of four populations in 1986. These estimates are substantially higher, especially for some stocks, than reported for recent years (SC/39/SM17; SC/37/SM12; SC/38/SM15; Wahlen, 1987). Total kill estimates were 24,000[1], 39,400, 56,700 and 129,500 from 1983 to 1986. Several reasons for the increases in 1986 were noted, including (1) increased fishing on dolphin schools, (2) larger catches of tuna per set, (3) higher proportions of night sets, (4) increased fishing on species and stocks with higher rates of incidental mortality (e.g., the common dolphin), and (5) higher proportions of (more vulnerable) juvenile dolphins in the kill of offshore spotted dolphins. Reasons 2–5 suggest that the numbers of dolphins killed per set or per ton of tuna captured, as analysed in SC/37/SM12, was substantially higher in 1986 than in recent years, although specific numbers are not given.

6.1.1.1 *Coverage of the international fleet*

Sampling intensity in 1986 was 30% of all fishing trips, substantially higher than in previous years. Coverage has increased from 13% in 1984 and 21% in 1985. Sampling was still higher for the US fleet, with 43% of the US versus 26% of the non-US trips being sampled. The coverage of the non-US fleet is, however, an improvement over the coverage in the period 1979–84, which from Table 2 of SC/36/SM17 was 33% of the sets on dolphins by US vessels versus 7% from the non-US fleet.

6.1.1.2 *Differences between US and non-US kill rates*

Possible differences in kill-per-set (KPS) rates for the US versus the non-US fleets were noted in SC/36/SM17, and the existence of such a difference was confirmed in 1984 (SC/37/SM12) for two statistical areas but not for five other areas. Other considerations were noted that made stratification by US versus non-US samples undesirable in that year because of sample-size limitations. However, concern was noted then about the representativeness of the sampling of non-US vessels up to 1984, especially in the two statistical areas where significant differences had been demonstrated between US and non-US KPS rates, and the problem was thought to be serious. There have been recent improvements in sample coverages of the non-US fleet, but the same estimation method (not stratifying by country) was used this year. It may now be possible to remedy this earlier-identified problem, or alternatively to conduct a new statistical test of differences in KPS rates. The continuing increase in the non-US participation in the fishery, in conjunction with differences in sampling fraction by nation, suggests that any differences in KPS rates would result in biased estimates of the kill. Previously-identified lower KPS rates for US vessels would suggest that the current estimates of total kill could be biased downward.

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[1] Estimate for US plus 1/5 of estimate for non-US 1979–83 from Table 4.

6.1.1.3 *Effects of school size and age structure*

It was not noted if dolphin school sizes were larger in 1986, although SC/39/SM9 suggests that school sizes may have increased steadily since 1983 for the northern offshore spotted, eastern spinner, and northern common dolphin populations. School size has been suggested in the past as positively correlated with kill rates. The possible effect of the fishing process on school size was noted in SC/37/SM12; analyses of this possibility was noted to be in preparation, but were not available during the meeting.

The possibility of an increased proportion of sub-adult animals in the kill is not evident in comparing Tables 4 or 5 of SC/39/SM1 with the corresponding tables in SC/37/SM1, although it was noted that the samples in the kill-composition papers may not have been representative of the kill. The basis for the statement about change in age structure of the catches in SC/39/SM12 should be given. The suggestion in the paper that it reflected an increase in the pre-adult fraction of the population suggests that the abundance of adult animals may have decreased, a particular concern given recent kill levels. The other suggestion that this is due to changes in the fishing areas or selectivity was also a concern to the sub-committee, suggesting possibly increasing impact of the fishery on the populations. The suggestion that this increase is due to increased recruitment requires more information than given.

6.1.1.4 *Possible revision of earlier estimates*

Because of increasing levels of kill reported here, it is important to compare new estimates with those for earlier years. The estimation procedure used has been applied to the data from 1984, 1985 and now 1986. This procedure would need to be applied to the data from before 1984 in order to make statistically valid comparisons (SC/37/SM12). Such estimates were not available to the sub-committee. However, differences in kill rates among countries that were identified in the 1979–84 data, and as were suggested during discussions during the meeting of the 1986 data, suggested to the sub-committee that kill estimates for earlier years that might be made without stratifying by country would be biased downward in proportion to the degree of involvement of countries other than the US and in proportion to the proportion of the fishing effort sampled.

In summary of the discussions on kill estimates, members noted that the problem of dolphin mortality in the ETP is two-fold. The sub-committee was interested firstly in the size and effects of the kill by species and stock, and secondly in ways in which mortality could be reduced. It noted that the first point was admirably addressed by SC/39/SM12 but that there was little information available on the second. Buckland briefly described technological assistance provided to the international fleet with the aid of UNEP funding. A report which addressed both practical efforts made to reduce mortality and the questions of differential kill rates among areas and fleets would be timely now that a much larger proportion of the non-US fleet was being sampled.

The sub-committee noted the valuable and very important increased participation in the international effort to assess and solve the tuna/dolphin problem and urged that the effort be continued and enlarged.

6.1.2 *Trends in abundance*

SC/39/SM9 presented new analyses that addressed some of the difficulties identified with earlier similar analyses and included data for more years. The sub-committee found it to be an excellent, very detailed analysis of a complex data set that revealed much about the status of dolphins involved in the fishery. The sub-committee was especially appreciative of the detailed development of the methods used, because that information allowed evaluation of the strengths and weaknesses of the analyses and the data set and provided considerable insight into the populations and the fishery.

Line transect analysis was applied to the sighting data collected by scientific technicians placed aboard tuna vessels. Encounter rates (total numbers of schools sighted per nautical mile searched by the fishermen) in each 1° square were used to stratify the abundance data, with strata defined to achieve homogeneous encounter rates averaged over neighbouring 1° squares to account for possible non-randomness in sampling. Data were divided into the resulting strata, and abundance estimated as the product in each strata of encounter rates, mean school size, and average effective search width using the 'smearing' procedures as in SC/39/Mi2. Estimates of population size are presented for eight populations of three species of dolphins from 1975 to 1986.

The authors noted a number of difficulties with these data for analysis by line transect techniques and described the methods used to accommodate these difficulties where possible. Several of the difficulties were not completely overcome, and with these in mind the authors suggested that the estimates should not be interpreted as absolute abundance estimates, but rather as indices that show trends in abundance. Under this interpretation the authors suggested that the abundance of northern offshore spotted dolphin, eastern spinner dolphin, and central common dolphins had all declined from 1975 to the early 1980s. The authors also noted that there was a suggestion in the estimates of increases in abundance for northern offshore spotted dolphin and for eastern spinner dolphin in the mid-1980s, although these estimates are difficult to interpret for the northern offshore spotted dolphin because of the apparently biased estimate for 1983. Omitting that point leaves little evidence of an increase. The estimate for the eastern spinner in 1986 is significantly higher than the estimate for 1981–84. The estimated increase is very much greater than could be expected for a dolphin population as a result of natural increase, although a confidence interval for the difference includes levels of increase that are biologically reasonable.

The sub-committee noted several general uncertainties with these analyses that make interpretation of the suggested trends difficult, relating to several factors noted below.

(1) Data collected during the commercial fishing process may be affected by: (a) large and small scale non-random searching patterns; (b) biases in estimates of angle to sighting caused by the searching process; (c) inter-annual changes in degree to which tuna vessels are fishing on dolphins; (d) inter-annual changes in

geographic location of searching effort; (e) the recent increase in use of helicopters for searching.

(2) Rounding errors may exist in estimation of sighting distance and angles.

(3) An unreasonably low estimate of abundance for the northern offshore population of spotted dolphin in 1983, during a major El Niño event, suggest that large changes in environmental processes induce biases in estimates of trends.

(4) The series of estimates for the eastern stock of spinner dolphins is unexpectedly smooth given the magnitude of the standard errors of the estimates.

(5) Unexplained patterns are apparent in estimates from the data in each quarter of each year, with higher estimates in the first and second quarters than in the third and fourth quarters in most years.

The sub-committee noted that the analytic methods that had been developed to accommodate some of the difficulties with assumptions were a great improvement in the analyses, but also noted that not all of the problems in the data had been resolved. Specific notice was given to non-random tuna vessel searching. It was felt that the stratification method used may address large scale non-randomness, although the statistical properties of the post-stratification procedure involving smoothing data in 1° squares by weighted average of data over a wide area were not well known. It was also felt, however, that this approach did not address small-scale non-randomness in search patterns with which several members had personal experience. While the smearing techniques used were thought to adequately address the errors in estimation of angles and distance, these techniques did not adjust for possible biases in estimation of the sighting angle that may result from the fishing process (for example, recording of angle after the vessel has turned toward the school). The effects of these errors would lead to overestimation of abundance.

The manner in which changes in the degree to which vessels are fishing on dolphins and inter-annual changes in geographic location of searching effort affect the estimates of trends in abundance is not clear, but such effects are likely large and unpredictable.

The sub-committee members noted with appreciation the great amount of information available to it on this problem. However, the increasing levels of kill estimated in recent years and the corresponding apparent decrease in abundance during the late 1970s are causes for concern. These suggested declines contradict the previous understanding of the status of these stocks (Smith, 1983), based on absolute abundance estimates from research platforms, estimated dolphin mortality levels from the beginning of the fishery in the early 1960s, and substantially reduced estimated dolphin mortality levels from the late 1970s and onward. The contradiction may be due to biases in estimates of dolphin kill levels historically or recently (possibly as the international composition of the fishery has changed), biases in the absolute abundance estimates used in Smith (1983), biases in the estimates of the trends of abundance in SC/39/SM9, or indirect effects of the fishing process on the life history of the dolphins.

The magnitude of the changes in the population size of one of the populations (the northern offshore spotted dolphin) suggested by SC/39/SM9 is large, from an average of 4.2 million in 1975–79 to an average of 2.9 million in 1980–82, a 30% estimated decline. Although the variability of each of the estimates is large, with coefficients of variation decreasing over time from 23% to 14%, Buckland suggested that these estimates provide good evidence of a decline. Taken in conjunction with estimates of approximate 40 to 60% reduction of this population from the early 1960s to mid to late '70s by Smith (1983), these estimates, if correct, suggest that there may be cause for concern about the present status of this population, as well as some other populations such as the eastern spinner.

It is important that additional studies be undertaken to resolve some of these uncertainties so that a comprehensive understanding of the status of the stocks can be obtained. In particular, the sub-committee recommended that analytical studies of fishing operations on a detailed basis be carried out, in line with the recommendations of the recent workshop on CPUE (SC/39/Rep2), to allow more detailed evaluation of the trends of abundance indicated in SC/39/SM9. The sub-committee recommended the reporting next year of indices of abundance from ongoing US research-vessel surveys, to provide calibration of the abundance indices derived from data collected during fishing operations.

6.2 Exploitation of small cetaceans in South America

The sub-committee received a preliminary report from Gaskin on the UNEP/IUCN–supported investigation of small cetacean involvements in fisheries in Peru (SC/39/SM10). The work began in 1985 and was completed this year. The field programme has covered ports along the entire coastline of Peru and extended into southern Ecuador and northern Chile. What had been thought to be primarily a problem of incidental kill of Burmeister's porpoise, *Phocoena spinipinnis*, (UNEP, 1985) has turned out to involve mainly the dusky dolphin, *Lagenorhynchus obscurus*, which comprised 83% of the carcasses examined. The species composition of the catch may have changed since it was first noted in the late 1960s. The dolphins are taken in offshore gillnets. Some of the take is incidental to a gillnet fishery, but some is also directed take. Some additional directed take is by purse seine and harpoon. The porpoise (12% of the specimens examined), on the other hand, are taken only incidentally, in an inshore gillnet fishery for sharks and rays. Several other species of dolphins and small whales are taken in smaller numbers, chief among them being the common dolphin, *Delphinus delphis*, and the bottlenose dolphin, *Tursiops truncatus*. Annual catches of small cetaceans as reported in official Peruvian catch statistics have ranged from about 500 tonnes to about 1,000 tonnes in recent years. The research team found the reported statistics to be consistent with results obtained in its field surveys. The statistics, however, do not include struck-but-lost adjustment. Efforts are underway to partition the weight figures to species and, ultimately, to numbers of animals. The impacts of the takes on the populations are unknown. At present there is no legal protection or management of small cetaceans in Peruvian waters. Gaskin agreed to provide further progress reports to the sub-committee as the analyses of the data are completed.

The sub-committee was provided with an update on exploitation of small cetaceans in Argentina (SC/39/SM3). There was no directed take during the period 1979–86 other than live-capture for exhibition. Species taken incidentally by fisheries are known to have included *Cephalorhynchus commersonii*, *Lagenorhynchus australis* and possibly included *Phocoena dioptrica*[1]. A lack of trained observers has prevented adequate coverage of the various fisheries along the very long coastline of Argentina.

6.3 Killer whale assessment

SC/39/SM8 and SC/39/SM19 reported the results of continued photographic identification studies of killer whales in Iceland and Norway, respectively. A preliminary report on the work in Iceland has been published (Lyrholm, Leatherwood and Sigurjónsson, 1987).

In 1986, vessel surveys off eastern and southern Iceland resulted in 37 observations of groups of killer whales, including 23 observations which resulted in the photographic identification of 111 individuals (SC/39/SM8). The total of individual killer whales photographically identified in Icelandic waters since 1981 is 143, of which 79 have been provisionally assigned to one of 6 pods. Maximum distance between resightings in Iceland was 160km.

In coastal waters at Lofoten, Norway, 18 individual killer whales were photographically identified in 1986, resulting in a total of 26 identified in Norway to date (SC/39/SM19). Of particular interest is the photographic re-identification of two killer whales observed off Möre in April 1984 and seen again 700km distant in Lofoten in September 1985.

There have been no photographic matches, to date, between the 143 individual killer whales identified off eastern Iceland and the 26 identified in Norwegian coastal waters. Moreover, preliminary analyses of acoustic recordings from the two areas have found no overlap in call types (SC/39/SM18). Further photographic and acoustic sampling in these and other areas of the North Atlantic should provide more conclusive evidence of stock relationships.

The report of a workshop on North Atlantic killer whales in May 1987 was made available for the sub-committee's information (SC/39/SM18). Although this document was not reviewed, the members noted with interest that: (1) the killer whale's former and recent distribution in the North Atlantic is much wider than was indicated earlier (*Rep. int. Whal. Commn* 32: 617–18); (2) the gestation period of three killer whales conceived and born in captivity was estimated, on the basis of patterns in hormone levels, as 17 months; and (3) the on-going age-determination work of A. Myrick and co-workers, using a sample of killer whale teeth which includes some labelled with tetracycline, may allow the calibration of layering patterns and improve preparation and reading techniques. The sub-committee was advised of plans to publish the workshop report and some of the presented papers in a book or special issue of a scientific journal. The report contained an estimate of about 190 killer whales in Icelandic coastal waters based on a capture-recapture analysis using photoidentification data.

Two papers on killer whales in Alaskan waters were available to the sub-committee. SC/39/SM6 was a summary of progress made from 1976 to 1986 in photographic identification studies in Prince William Sound. SC/39/SM6 was a catalogue of photographs of the 218 whales identified and assigned to pods in Southeast Alaska through 1986.

SC/39/SM4 contained information on killer whale distribution and exploitation in the Indian Ocean. The paper was submitted to the Scientific Meeting on the Indian Ocean Sanctuary.

6.4 Dall's porpoise assessment

Two major colour morphs of *Phocoenoides dalli* (*truei*-type and *dalli*-type) occur in the waters around Japan, and paper SC/39/SM11 treated results of nine whale sighting cruises, in order to examine geographic distribution and estimate abundance of the two morphs.

The minimum estimate of abundance of the *dalli*-type in the Sea of Japan/Okhotsk Sea area was about 32,000 (CV=0.225). The size of the total *truei*-type population is about 56,000–90,000 individuals.

The sub-committee noted the excellent quality of the analyses and expressed appreciation for the work that had gone into them. Some suggestions were made for further analysis of the sightings data, so that a more robust estimate of abundance might be obtained. In particular, it was suggested that the sighting angle and distance data should be 'smeared' before analysis, and that further assessment of which line transect model(s) to use might prove useful. In addition, there was discussion of the relevance of the location of cruise tracks to the mapped distribution of the two colour morphs. The sub-committee recommended that catches of *P. dalli* be sampled to determine the proportion of each colour type in the catches and that biological studies of the catches be carried out. In conjunction with stock size estimates and information on biological parameters, this should enable assessment of the impact of the present catches (10,782 in 1986 – SC/39/ProgRep Japan) on the two populations to be carried out.

6.5 Small cetaceans in the Indian Ocean Sanctuary

Two papers which had been submitted to the Indian Ocean Sanctuary meeting in the Seychelles in February 1987 were also made available to the sub-committee. SC/39/SM4 reviewed information on the distribution and exploitation of six species in the Indian Ocean: *Orcinus orca*, *Pseudorca crassidens*, *Globicephala melaena*, *G. macrorhynchus*, *Feresa attenuata* and *Peponocephala electra* (mostly juveniles). SC/39/SM5 reviewed information on Risso's dolphin, *Grampus griseus*. It was noted that Risso's dolphins (mostly juveniles) comprised about 25% of the 858 small cetaceans examined that were taken off Sri Lanka during 1981–6 and that a similar proportion of cetacean sightings off Sri Lanka involved this species.

7. OTHER BUSINESS

7.1 Takes of small cetaceans in 1986

Information on takes (directed, incidental and live-capture) available to the meeting is summarised in Appendix 2.

7.2 Progress on requests for catch statistics in 1986

The sub-committee noted the submission of progress reports containing data on small cetacean catches by the following nations that did not submit progress reports last year: Argentina, France and Sweden. These new data submissions were welcomed. Reports for other IWC member nations known to take small cetaceans remain non-existent or incomplete. The sub-committee notes that submission of catch statistics by calendar year would facilitate consideration and summarization of the data.

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[1] *Editor's note.* Subsequent to the meeting Perrin drew attention to the proposed placement of the spectacled porpoise, *Phocoena dioptrica*, into a new genus, *Australophocaena* (Barnes, L.G., 1985. Evolution, taxonomy and antitropical distributions of the porpoises (Phocoenidae, Mammalia). *Mar. Mamm. Sci.* 1(2): 149–65).

7.3 Priority topics for 1988 meeting

It is proposed that next year's meeting of the sub-committee focus on a review of population biology and assessment of the beaked whales, in addition to reviewing progress relative to past recommendations. The sub-committee notes that the several major studies in progress of pilot whale populations in the North Atlantic will be completed and draft papers available by 1989 and proposes that the work be reviewed at the 1989 meeting.

7.4 Workshop on incidental take of cetaceans in gillnet fisheries

In 1985 the Committee recommended that a workshop meeting be held to review new and expanding gillnet fisheries that take cetaceans incidentally (*Rep. int. Whal. Commn* 36: 37), to investigate how and why entanglement occurs; to estimate mortality and assess its impact on cetaceans, and to consider the possible ways of reducing the mortality of cetaceans, including the large whales, in gillnets. The workshop was tentatively scheduled for Autumn 1986 in Seattle but was not convened, primarily because of funding problems. The workshop is still needed, as pointed out in SC/39/Rep1. Perrin reported that the workshop is included in the draft Action Plan of the IUCN Cetacean Specialist Group for 1988–1991, and an invitation offering to host the meeting has been extended by the Southwest Fisheries Center in La Jolla, California.

7.5 Publication of documents

A list of documents to be considered for publication was submitted to the Editorial Board.

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Appendix 1

AGENDA

1. Election of Chairman
2. Appointment of rapporteurs
3. Adoption of agenda
4. Review of available documents and reports
5. Review of life histories and status of populations of pilot whales, *Globicephala* spp
    5.1 North Atlantic populations of *Globicephala melaena*
        5.1.1 Stock identity and distribution
        5.1.2 Abundance
        5.1.3 Migration
        5.1.4 Life history
        5.1.5 Exploitation
        5.1.6 Status
    5.2 Other populations of *G. melaena*
    5.3 Populations of *G. macrorhynchus*
6. Review of new information on other exploited small cetaceans
    6.1 Tuna/dolphin problem in eastern tropical Pacific
    6.2 Exploitation of small cetaceans in South America
    6.3 Killer whale assessment
    6.4 Dall's porpoise assessment
    6.5 Small cetaceans in the Indian Ocean Sanctuary
7. Other business
    7.1 Takes of small cetaceans in 1986
    7.2 Progress on requests for catch statistics in 1986
    7.3 Priority topics for 1988 meeting
    7.4 Workshop on incidental take of cetaceans in gillnet fisheries
    7.5 Publication of documents

Appendix 2

REPORTED CATCHES OF SMALL CETACEANS IN 1986

Species		Argentina[1]	Australia[2]	Canada[3]	Denmark[4]	France[5]	Japan[6]	Sweden[7]	USA[8]	USSR[9]	Other	Total
Baird's beaked whale, Berardius bairdii	D	–	–	–	–	–	40	–	–	–	–	40
Narwhal, Monodon monoceros	D	–	–	263	x	–	–	–	–	–	–	263+x
White whale, Delphinapterus leucas	D	–	–	700	7+x	–	–	–	x	178	–	885+x
	I	–	–	–	–	–	–	–	1	–	–	1
False killer whale, Pseudorca crassidens	D	–	–	–	–	–	2	–	–	–	–	2
	I	–	x	–	–	–	1	–	–	–	x[10]	1+x
Killer whale, Orcinus orca	D	–	–	–	–	–	8	–	x	–	16[11],x[10]	24+x
Pygmy killer whale, Feresa attenuata	I	–	–	–	–	–	–	–	–	–	x[12]	x
Long-finned pilot whale, Globicephala melaena	D	–	–	–	1,709	–	–	–	–	–	–	1,709
	I	x	–	–	–	–	–	–	x	–	–	x
	L	–	–	–	–	1	–	–	–	–	–	1
Short-finned pilot whale, G. macrorhynchus	D	–	–	–	–	–	375	–	–	–	x[12-14]	375+x
	I	–	–	–	–	–	3	–	–	–	x[10]	3+x
Melon-headed whale, Peponocephala electra	D	–	–	–	–	–	–	–	–	–	x[10,13]	x
	I	–	–	–	–	–	–	–	–	–	x[10]	x
Pacific white-sided dolphin, Lagenorhynchus obliquidens	D	–	–	–	–	–	4	–	–	–	–	4
	I	–	–	–	–	–	33	–	–	–	–	33
Atlantic white-sided dolphin, Lagenorhynchus acutus	D	–	–	–	195	–	–	–	–	–	–	195
	I	–	–	–	–	–	–	–	2	–	–	2
Dusky dolphin, L. obscurus	D	–	–	–	–	–	–	–	–	–	x[14]	x
	I	x	–	–	–	–	–	–	–	–	x[14]	x
Peale's dolphin, L. australis	D	x	–	–	–	–	–	–	–	–	–	x
	I	x	–	–	–	–	–	–	–	–	–	x
Bottlenose dolphin, Tursiops truncatus	D	–	–	–	–	–	230	–	–	–	–	230
	I	x	450+x	–	–	3	–	–	2–4	–	x[14]	455–457+x
	L	2	–	–	–	–	–	–	1	–	–	3
Spotted dolphin, Stenella attenuata	D	–	–	–	–	–	693	–	–	–	–	693
	I	–	x	–	–	–	–	–	x[17]	–	67,245[18]	67,245+x
Spinner dolphin, Stenella longirostris	I	–	260+x	–	–	–	–	–	x[17]	–	31,306+x[18,12]	31,566+x
Striped dolphin, Stenella coeruleoalba	D	–	–	–	–	3	2,918	–	–	–	–	2,921
	I	–	–	–	–	4+x	82	–	x[17]	–	x[18]	86+x
Common dolphin, Delphinus delphis	D	–	–	–	–	2	1	–	–	–	–	3
	I	–	–	–	–	5+x	12	–	x[17]	–	25,794+x[18,14]	25,811+x
Fraser's dolphin, Lagenodelphus hosei	I	–	–	–	–	–	–	–	x[17]	–	x[18]	x
N. right whale dolphin, Lissodelphis borealis	I	–	–	–	–	–	154	–	–	–	–	154
Commerson's dolphin, Cephalorhynchus commersonii	I	29+x	–	–	–	–	–	–	–	–	–	29+x
Risso's dolphin, Grampus griseus	I	–	–	–	–	1	2	–	–	–	2+x[19]	5+x
Franciscana, Pontoporia blainvillei	I	x	–	–	–	–	–	–	–	–	–	x
Humpback dolphin, Sousa chinensis	I	–	x	–	–	–	–	–	–	–	–	x
Harbour porpoise, Phocoena phocoena	D	–	–	–	–	–	30	–	–	–	–	30
	I	–	–	–	x	–	36	19	4+x	–	–	59+x
Burmeister's porpoise, P. spinipinnis	I	–	–	–	–	–	–	–	–	–	x[14]	x
Dall's porpoise, Phocoenoides dalli	D	–	–	–	–	–	10,534	–	–	–	–	10,534
	I	–	–	–	–	–	248	–	–	–	–	248
Spectacled porpoise, Phocoena dioptrica	I	x	–	–	–	–	–	–	–	–	–	x
Vaquita, P. sinus	I	–	–	–	–	–	–	–	–	–	x	x
Unidentified species	D	–	–	–	–	–	10	–	–	–	–	10
	I	–	x	–	–	x	2,055	–	151–538[17]	–	5,114+x[12,14,18,10]	7,320–7,707
Sub-total	D	x	–	963	1,927+x	5	14,845	–	x	178	x	17,918+x
	I	31+x	710+x	–	x	14+x	2,626	19	160–549+x	–	129,461+x	133,018–133,407+x
	L	2	–	–	–	1	–	–	1	–	–	4
TOTAL		33+x	710+x	963	1,917+x	19+x	17,471	19	161–550+x	178	129,461+x	150,940–151,329+x

* In response to requests in the Commission meeting last year, to clarify the status of the statistics presented, official statistics have been taken to be those provided in National Progress Reports or official catch records submitted to the Secretariat. No catches were reported in SC/39/ProgReps Brazil, Iceland, Korea, Netherlands, Norway or UK. Values given in scientific papers to the Committee are provided for information only and their sources indicated; these are given under the heading 'other'. Also in response to comments within the Commission, catches have been presented by nation, rather than ocean area, except in the case of the data submitted by the IATTC for the eastern Tropical Pacific. In this latter case, the submitted estimated catches are not broken down by country but a summed total incidental catch for the following countries is given: Costa Rica, Ecuador, El Salvador, Mexico, Panama, Spain, USA, Vanuatu and Venezuela.

Key: D = direct take: I = incidental capture; L = live capture; x = catches known to occur, but no current information available on levels.

Footnotes: (1) SC/39/ProgRep Argentina: information that catches took place given but precise values not provided for all species and areas. (2) SC/39/ProgRep Australia and SC/38/SM14. (3) SC/39/O 29 (Progress Report from Canada). (4) SC/39/ProgRep Denmark: information that catches took place given but precise values not provided for all species and areas. (5) SC/39/ProgRep France: information that catches took place given but precise values not provided for all species and areas. Values in the table are correct for the calendar year 1986. They are not identical to those in the Progress Report which covers 1985/86. (6) SC/39/ProgRep Japan: a few live captures are included in incidental or directed catches. (7) SC/39/ProgRep Sweden. (8) SC/39/ProgRep USA: information that catches took place given but precise values not provided for all species and areas. Killer whales have probably been shot by fishermen to protect their longline catches of black cod (SC/39/SM6). See note 17 regarding ETP catches. (9) SC/39/ProgRep USSR: information that catches took place given but precise values not provided for all species and areas. (10) SC/39/SM4: incidental catches in gillnets off Sri Lanka, or harpooned. (11) SC/39/SM18: Table 1 (Greenland). (12) SC/39/O 1: a few directed catches in St Lucia. (13) SC/39/SM4: a few killed annually by Lamalera whalers. (14) SC/39/SM10: taken off Peru, some tens to some hundreds. (15) SC/39/SM3: harpooned for crab bait, or incidental catches. (16) SC/38/SM15. (17) The US National quota (over-subscribed by about 200) for the dolphin kill in the purse-seine fishery in the ETP was 20,500. The values in SC/39/ProgRep USA (Table 2) are only for the kill observed by US/NMFS technicians. The values in SC/39/SM1 are for composition of the observed kill. The extrapolation procedures used by the USA to monitor their quota regulation are not strictly comparable to the IATTC procedure (SC/39/SM12), and thus subtraction of the US estimated kill from the total IATTC estimate gives only a very rough guide to the non-US kill. (18) SC/39/SM12: incidental catches in the ETP, total estimation for seiners from Costa Rica, Ecuador, El Salvador, Mexico, Panama, Spain, USA, Vanuatu and Venezuela. (19) SC/39/SM5.

Appendix 3

USE OF TRACE COMPOUNDS TO DISCRIMINATE HOME RANGES IN CETACEANS

Alex Aguilar

Because mammals incorporate pollutants mostly via food, their body load of xenobiotic compounds reflects the chemical characteristics of the environment in which they live and feed. In turn, the chemical load of a given water mass depends on relative and absolute quantities of pollutants discharged in neighbouring areas, distance to pollutant sources, food chain complexity, physical environmental parameters such as temperature or water current regimes, and possibly other factors. All these factors produce wide variation of pollutant loads in different water masses, often on a short distance scale.

Logically, animals inhabiting environments with different pollutant profiles are likely to carry distinguishable pollutant burdens, and these burdens may help to ascertain whether two or more sample groups have more or less stable allopatric distributions.

Following this line of thinking, pollutant burdens have been used to study migratory patterns or geographical segregation in fishes, birds, and some marine mammals (Krygier and Pearcy, 1977; Dutil *et al.*, 1985; Calambokidis, 1986). This method has poor relation or no relation at all to genetics, so it will not be useful to discriminate populations that are genetically independent but which feed in largely overlapping areas or in areas with very similar pollutant loads. It may be of utility, however, when the research deals with groups of animals occupying different water masses during most of their life cycle. This applies not only to most typical genetically isolated populations, but also to components of homogeneous interbreeding populations which are partially allopatric (for example, sperm whales of different age, sex, or reproductive condition).

However, tissue pollutant concentrations of cetaceans are not simply a direct mirror image of the pollutants present in the water. Many factors unrelated to geographical distribution may affect the pollutant levels of certain individuals, groups of individuals, or even entire population components, making it relatively easy to find artifactual differences between groups due more to heterogeneities or inconsistencies in sampling than to a real geographical segregation. These factors should be examined before attempting any comparison and taken into account when sampling or when analysing results.

In the case of organochlorines, Aguilar (1987) has examined the significance of the most important perturbing factors and discussed the limitations and potentials of these compounds for discriminating marine mammal groups with allopatric home ranges. Factors identified were age, sex, nutritional state, reproductive condition, trophic level (which may be heterogeneous within an otherwise homogeneous, population), excretory and metabolic activity, and tissue composition. These factors do not affect all compounds the same, so not only may their absolute tissue concentrations vary but, also, the ratios between compounds may be subject to a definite and often predictable variation. Therefore, the selection of certain compounds or ratios between compounds will be determined by the characteristics of the sample collected and by the characteristics of the groups to be distinguished. For example, the tDDT/PCB ratio is known to increase with distance from pollution sources (and thus, from the coast), but to decrease with age in females due to differential reproductive transfer to offspring. Therefore, it may be extremely useful in differentiating offshore and inshore populations of the same species (such as bottlenose dolphins or Bryde's whales), provided that the female samples to be compared have similar age compositions. By the same token, some ratios may be misleading under inconsistent sampling regimes or in populations which are suspected to be affected by unmonitored sources of variation.

However, the effect of some factors is still to be ascertained. It is not clear, for example, how important the interactions are between different compounds in enhancing or diminishing the degradative capability of the animals. Most importantly, the use of stranded cetaceans (often diseased and with low fat reserves) to characterise levels of pollutants in marine mammal populations has been repeatedly questioned (Aguilar, 1984), but it is still unclear whether it is reliable or not.

Unfortunately, similar studies are not available for other potentially useful chemical indicators such as heavy metals, trace elements, or radionuclides, all already used in population discrimination of marine organisms other than cetaceans. Research is needed here. Moreover, since the most powerful discrimination capability will undoubtedly come from the comparison of pollutant loads integrating different families of compounds, research is also needed to understand the interactions and the sources of variation of ratios derived from chemicals belonging to different families (for example, combinations of selected heavy metals and organochlorines).

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Dolphins, Porpoises, and Whales

An Action Plan for the Conservation of Biological Diversity: 1988-1992

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Foreword

The cetaceans are the major conservation flagship group of the marine environment, let alone the broader mammal world, and, as such, they draw considerable attention from environmentalists, the media, and the public at large.

With this Action Plan, one of many being produced for IUCN's Species Survival Commission by its active Specialist Groups, we have scientifically based schemes and plans laid out for conservation of both the whales and the smaller cetacean species.

It is with considerable pride that I write this short foreword, as this Specialist Group, under the most able leadership of Bill Perrin, has consistently led the field, both in the Group's members' individual capacities and as a Group, in ensuring that IUCN has the best possible data available on which to lead the conservation thrust for these majestic creatures worldwide. The Plan provides for the next phase, one might say, for conservation action. It must be funded and the Action Plan turned into action.

I would like to take this opportunity to thank and congratulate the Cetacean Specialist Group on their Action Plan, and commend its findings for immediate funding.

Grenville Ll. Lucas
Chairman
IUCN Species Survival Commission

Introduction

Man has not yet driven any cetacean species to extinction. This may change, however, and soon. For some species, only a few hundred individuals remain. For others, populations of larger or unknown size may be declining rapidly. The primary goal of the Cetacean Specialist Group in putting forward this action plan is to precipitate activity to prevent extinction of the species and populations currently in danger. The proposed actions also aim to promote sustainable relationships between cetaceans and people, in order to secure the long-term future for all cetacean species and populations.

This plan focuses on the small cetaceans, in particular the river dolphins. There are several reasons for this focus. First, the most endangered species are small cetaceans. With the possible exception of the northern right whale, none of the great whales are in imminent danger of extinction. However, some of the river dolphins face extinction in this century unless present trends are reversed. Second, the river dolphins are largely tropical and therefore occur entirely within the boundaries of the developing nations, where human population growth is the greatest and environmental conservation is most difficult and in early stages of development. This problem is exacerbated by the fact that riverine habitat is restricted and highly vulnerable to degradation.

An additional reason for placing emphasis in this plan on the small cetaceans is that heretofore conservationists working to protect cetaceans have given most attention to the great whales. This has resulted in a substantive increase in much-needed research, legislation, and management, and in relatively well-organized systems of conservation monitoring and feedback. The small cetaceans have received far less attention, despite the fact that many species face severe problems. There are many problems in conservation of the great whales yet to be solved, especially those regarding the regulation of whaling, but many organizations and agencies are working to solve the problems. This is not as true for the small cetaceans.

Secondarily, this plan emphasizes coastal small cetaceans. By comparison with pelagic habitats, coastal habitats are more restricted and more vulnerable to degradation and depletion.

The plan considers endangered populations as well as species and formally designated subspecies. Formal description and naming of subspecific taxa have not been a common practice in cetacean systematics in recent years. For example, Robineau (1986) suggested that the very distinctive Kerguelan race of *Cephalorhynchus commersonii* be accorded "subspecific status" but did not formally describe a subspecies or propose a trinomial. The morphologically distinct populations that have been defined but not formally named for several small cetaceans correspond in degree of distinctness to the entities in terrestrial mammals that have received subspecific scientific names. Thus, an endangered small-cetacean population that might find a place in lists of endangered "species" were it described as a subspecies does not receive such recognition. For this reason, the plan includes not only species that are formally designated in the Red List as Endangered, Vulnerable, etc., but also those nonlisted species for which one population or more may be in peril. The implication is that in these cases potentially significant genetic variability and unique components of regional ecosystems are at risk.

Acknowledgments

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Classification

As for most major groups, there is a certain amount of flux in the taxonomy of the cetaceans. They currently comprise 77 species: 66 toothed whales (Odontoceti) and 11 baleen whales (Mysticeti). The treatment here (Table 1) is not meant to be definitive or revisionary, but only to reflect the compiler's perception of mainstream thinking about the species and populations. The taxa above the species level follow Barnes et al. (1985), as later revised by Barnes (1985a,b). The monophyly of the cetaceans is now firmly established based on several lines of evidence (Barnes 1984, Barnes et al. 1985) and the odontocetes and mysticetes accordingly are included in the single order Cetacea. The species largely follow Honacki et al. (1982) and Jones et al. (1986) and incorporate revisions of the spotted dolphins by Perrin et al. (1987a) and the porpoises and platanistoid dolphins by Barnes (1985a,b). Treatment of the right whales follows Brownell et al. (1987). The first-listed common names of the species follow IWC (1977, 1980-1988), with minor changes (Perrin et al. 1987a, Perrin and Brownell in press).

Table 1. Classification of the living cetaceans, order Cetacea.

Suborder Odontoceti	
Superfamily Platanistoidea	
Family Platanistidae	
Platanista gangetica	Ganges river dolphin, Ganges susu
Platanista minor	Indus River dolphin, Indus susu
Family Pontoporiidae	
Subfamily Lipotinae	
Lipotes vexillifer	baiji, Yangtze or Chinese river dolphin
Subfamily Pontoporiinae	
Pontoporia blainvillei	franciscana, cachimbo, La Plata dolphin
Family Iniidae	
Inia geoffrensis	boto, boutu, bufeo, Amazon river dolphin
Superfamily Delphinoidea	
Family Monodontidae	
Subfamily Orcaellinae	
Orcaella brevirostris	Irrawaddy dolphin, pesut
Subfamily Delphinapterinae	
Delphinapterus leucas	white whale, beluga
Subfamily Monodontinae	
Monodon monoceros	narwhal
Family Phocoenidae	
Subfamily Phocoeninae	
Phocoena phocoena	harbor porpoise
Phocoena spinipinnis	Burmeister's porpoise
Phocoena sinus	vaquita, Gulf of California harbor porpoise
Neophocaena phocaenoides	finless porpoise
Subfamily Phocoenoidinae	
Australophocaena dioptrica	spectacled porpoise
Phocoenoides dalli	Dall's porpoise
Family Delphinidae	
Subfamily Steninae	
Steno bredanensis	rough-toothed dolphin
Sousa chinensis	Indopacific hump-backed dolphin
Sousa teuszii	Atlantic hump-backed dolphin
Sotalia fluviatilis	tucuxi
Subfamily Delphininae	
Lagenorhynchus albirostris	white-beaked dolphin
Lagenorhynchus acutus	Atlantic white-sided dolphin
Lagenorhynchus obscurus	dusky dolphin
Lagenorhynchus obliquidens	Pacific white-sided dolphin
Lagenorhynchus cruciger	hourglass dolphin
Lagenorhynchus australis	Peale's dolphin
Grampus griseus	Risso's dolphin
Tursiops truncatus	bottlenose dolphin
Stenella frontalis	Atlantic spotted dolphin
Stenella attenuata	pantropical spotted dolphin
Stenella longirostris	spinner dolphin
Stenella clymene	clymene dolphin
Stenella coeruleoalba	striped dolphin
Delphinus delphis	common dolphin
Lagenodelphis hosei	Fraser's dolphin
Subfamily Lissodelphinae	
Lissodelphis borealis	northern right whale dolphin
Lissodelphis peronii	southern right whale dolphin
Subfamily Cephalorhynchinae	
Cephalorhynchus commersonii	Commerson's dolphin
Cephalorhynchus eutropia	black dolphin, Chilean dolphin
Cephalorhynchus heavisidii	Heaviside's dolphin
Cephalorhynchus hectori	Hector's dolphin
Subfamily Globicephalinae	
Peponocephala electra	melon-headed whale, electra dolphin
Feresa attenuata	pygmy killer whale
Pseudorca crassidens	false killer whale
Orcinus orca	killer whale
Globicephala melas	long-finned pilot whale
Globicephala macrorhynchus	short-finned pilot whale
Superfamily Ziphioidea	
Family Ziphiidae	
Tasmacetus shepherdi	Shepherd's beaked whale
Berardius bairdii	Baird's beaked whale
Berardius arnuxii	Arnoux's beaked whale
Mesoplodon pacificus	Longman's beaked whale
Mesoplodon bidens	Sowerby's beaked whale
Mesoplodon densirostris	Blainville's beaked whale
Mesoplodon europaeus	Gervais' beaked whale
Mesoplodon layardii	strap-toothed whale
Mesoplodon hectori	Hector's beaked whale
Mesoplodon grayi	Gray's beaked whale
Mesoplodon stejnegeri	Stejneger's beaked whale
Mesoplodon bowdoini	Andrews' beaked whale
Mesoplodon mirus	True's beaked whale
Mesoplodon ginkgodens	ginkgo-toothed beaked whale
Mesoplodon carlhubbsi	Hubbs' beaked whale
Ziphius cavirostris	Cuvier's beaked whale
Hyperoodon ampullatus	northern bottlenose whale
Hyperoodon planifrons	southern bottlenose whale
Superfamily Physeteroidea	
Family Physeteridae	
Subfamily Physeterinae	
Physeter macrocephalus	sperm whale
Family Kogiidae	
Kogia breviceps	pygmy sperm whale
Kogia simus	dwarf sperm whale
Suborder Mysticeti	
Family Balaenidae	
Balaena mysticetus	bowhead whale
Eubalaena australis	southern right whale
Eubalaena glacialis	northern right whale
Family Neobalaenidae	
Caperea marginata	pygmy right whale
Family Eschrichtiidae	
Eschrichtius robustus	gray whale
Family Balaenopteridae	
Subfamily Balaenopterinae	
Balaenoptera acutorostrata	minke whale
Balaenoptera borealis	sei whale
Balaenoptera edeni	Bryde's whale
Balaenoptera musculus	blue whale
Balaenoptera physalus	fin whale, finback
Subfamily Megapterinae	
Megaptera novaeangliae	humpback whale

The Problems Faced by Cetaceans

The number and complexity of factors preventing effective conservation of whales, dolphins, and porpoises are ever increasing. As the world human population booms and industrialization proceeds, there are shifts in the types of problems that are the most immediate and urgent, but the old problems do not necessarily disappear. Indigenous peoples still take whales and dolphins with harpoons; in some areas direct exploitation takes place side-by-side with degradation of habitat by modern petroleum and hydroelectric developments and development of crucial wetlands.

It is also becoming more difficult to identify and assess the problems in time to effect solutions. Industrial and agricultural development, especially, can operate to the detriment of cetaceans in subtle or hidden ways that often are recognized only after much damage has been done or after the momentum of development is so great that conservation of the mammals becomes impossible or impractical. Thus it is very important that the level of action addressing such problems increase now, because there will be even more and difficult problems to cope with in the future.

And, of course, there is the moral dilemma created by attempts to balance the short-term welfare and interests of specific human populations with the longer-term benefits of conserving species and ecosystems. Such considerations permeate nearly every problem of conservation of cetaceans. The policy of the Cetacean Specialist Group (CSG) on such conflict is that of IUCN, i.e., to promote rational utilization and management on a sustainable basis, recognizing that decisions about the relative importance to be given to wildlife conservation and short-term human welfare must rest with national peoples and governments. These goals are also embodied in the UNEP Global Plan of Action for Marine Mammals (FAO/IUCN/IWC/UNEP 1985, Nielsen 1986). There is much correspondence between the two plans. Our main concerns in the CSG are to identify the most critical and immediate conservation problems and help prevent extinction of species and populations wherever such efforts are possible and welcomed.

Dall's porpoise *(Phocoenoides dalli)* are harpooned in large numbers in the coastal waters of northern Japan. (Photograph by W. F. Perrin)

Direct Exploitation

To date, the main danger faced by the great whales has been overhunting. Whaling in the last hundred years has greatly reduced the populations of most species. Most whaling is now regulated through the IWC, with the stated management goal of sustainable exploitation. However, as explained lucidly by Holt (1986), it has been extremely difficult to determine what is sustainable, and modern exploitation in practice has seriously overshot sustainable levels in many cases and resulted in further depletion of the whale stocks. An IWC-mandated moratorium on commercial whaling is in effect until at least 1990, to provide an interval during which better ways of assessing the whale populations and the impacts of whaling can be developed and overexploited whale stocks can be given a chance to recover. It is to be expected that large-scale commercial whaling will recommence at some point; the resources are too extensive and valuable to escape systematic exploitation for long. In point of fact, substantial "research whaling" that could be construed as thinly disguised commercial whaling by some nations has continued during the supposed moratorium.

This action plan focuses on the small cetaceans, which also are exploited directly. Much of the take is for subsistence. Subsistence hunting can also deplete a population; for example, as noted below in the section on status of populations, several white whale stocks in Canada have been severely depleted by native hunters; other exploited populations of white whales in the USSR and populations of narwhals and harbor porpoise in Canada and Greenland are of unknown status. While the takes from such populations are for subsistence by indigenous hunters, growing human populations and the increasing use of modern technology (for example, rifles) have caused some hunts to exceed the long-standing levels of indigenous harvests in some regions. In other small-cetacean fisheries for subsistence, recent takes have fluctuated around levels that have existed for very long periods of time, for example in the Faroe Islands, where catches of pilot whales comparable to current catches have occurred cyclically over the last 500 years or more (Joensen and Zachariassen 1982, Hoydal 1986). In even these cases, however, downward trends in abundance could be masked by changes in fishing methods and intensity, and a long history of exploitation cannot be assumed to indicate necessarily that no problem exists.

Most of the remaining commercial directed fisheries for small cetaceans are operated out of Japan (IWC 1987b). Small whaling vessels equipped with harpoon guns take short-finned pilot whales from local stocks and Baird's beaked whales; smaller boats take Dall's porpoise, pilot whales, and dolphins of several species with hand harpoons; and drive fisheries annually capture thousands of dolphins and small whales, mainly striped dolphins, spotted dolphins, bottlenose dolphins, common dolphins, pilot whales, and false killer whales (Anon. 1987). Some of these takes are large enough to lead to concern about possible depletion of populations (see section on status of species and populations). It

Incidental kills in tuna purse seines have reduced the population of the eastern spinner dolphin (a morphologically distinct race of *Senella longirostris* endemic to the eastern Pacific) to less than half its original size. (Photo by J. A. Thompson, courtesy of Nu Venture Films) is possible that the demand for small-cetacean meat in Japan may increase as the supplies of whale meat decline because of the moratorium on commercial exploitation of the great whales. Such an increased demand would increase the pressure on the populations of dolphins, porpoise, and small whales.

A special category of directed fishery that is unsettling in its implications is that in which incidental take becomes transformed into a directed fishery. This has happened in Peru (Gaskin et al. 1987), where some incidental catch of dolphins and porpoises in coastal gillnet fisheries for sciaenids and sharks has been known to occur since at least the 1960s (Mitchell 1975); the meat was sold locally for human consumption. In the 1970s, unfavorable oceanographic conditions combined with overfishing to drive the Peruvian stocks of anchoveta to near extinction. The anchoveta fishery was at the time the largest fishery in the world, and its collapse put thousands of fishermen out of work. It now appears that many of these fishermen shifted to using gillnets to hunt dolphins, in particular *Lagenorhynchus obscurus*, exploiting the market created previously by the sale of dolphins caught incidentally in other fisheries. The catch of dolphins in the directed fishery may now exceed 10,000 in some years and may be sufficient to endanger the population(s). By-catches of dolphins and porpoises occur in hundreds of gillnet and purse-seine fisheries around the world (discussed below); the meat is marketed in many regions. The Peruvian example suggests that economic dislocations could well cause the fishermen to shift from smaller accidental to larger directed takes imperiling the cetacean populations. The likelihood is increased by the fact that such shifts are most likely to happen in the least developed and most impoverished and isolated parts of the world and thus often escape notice and regulation.

Even very small directed catches can be significant if the species or population is already depleted. For example, river dolphins are still hunted (illegally) in India, Pakistan, and Nepal (Perrin and Brownell in press), where the remaining populations are either critically endangered or rapidly declining toward that condition. In such cases the catches, although small, are obviously significant.

Incidental Catch in Fisheries

By far the largest takes of cetaceans today are by-catches. For example, in 1986 the international fleet of tuna seiners in the eastern tropical Pacific killed an estimated 129,000 dolphins, primarily *Stenella attenuata*, *Stenella longirostris*, and *Delphinus delphis* (Allen 1985, Hall and Boyer 1987), and gillnet fisheries for salmon and squid operated by several nations in the North Pacific may have killed as many as 16,000 Dall's porpoise annually in recent years (Dolan 1987). In both these cases the incidentally caught mammals are not utilized but rather thrown back into the sea. There are many other gillnet fisheries around the world that take small cetaceans (and some great whales) incidentally. In the developed nations, the by-catch is usually discarded or retained for scientific analysis only (for example in California—DeMaster et al. 1985, Barlow 1987); in less prosperous nations the catch is usually marketed locally for human consumption (for example, in Sri Lanka, where as many as 42,000 dolphins and small whales, mainly *Stenella longirostris*, *Stenella coeruleoalba*, *Stenella attenuata*, *Tursiops truncatus*, and *Grampus griseus*, are taken annually in gillnets as by-catch and marketed—Alling 1985). As noted above, such incidental catches can easily become directed catches. Fisheries that take or could take cetaceans incidentally are listed and briefly described in an excellent recent worldwide review of interactions between marine mammals and fisheries commissioned by FAO (Northridge 1984).

The impacts of the incidental catches on the populations are unknown in nearly all cases. In the case of the largest known kills, in the tuna fishery in the eastern tropical Pacific, there is little doubt that some of the dolphin populations have declined. However, debate continues about the extent of the declines and whether or not the populations are continuing to decline (Smith 1983, Buckland and Anganuzzi 1987, IWC 1988). Current assessment efforts for that fishery are concentrating on detection of population trends rather than on estimating absolute abundance and degree of depletion. Many of the catches in other fisheries are large enough that they may be non-sustainable; such fisheries must be considered to be dangerous to the well-being of populations until they are shown not to be. As in the case of directed takes, even small incidental takes can be dangerous to a severely depleted species or population. An example is the baiji in the Yangtze River (Perrin and Brownell in press), which is accidentally snagged in small but significant numbers on bottom long lines set for fish.

Bottlenose dolphins *(Tursiops truncatus)* and other dolphins and small whales are taken incidentally in gillnet fisheries around Sir Lanka. (Photograph by S. Leatherwood)

Competition and Culls

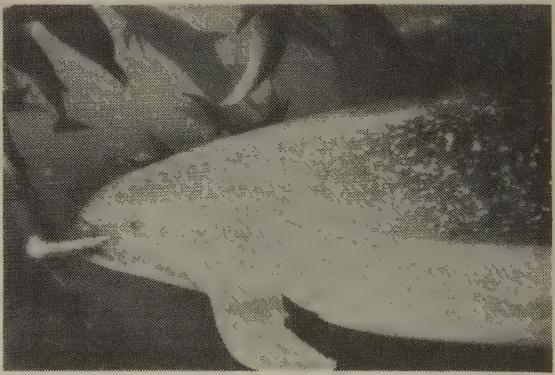
There are at least two situations in which cetaceans have been suspected of competing with fishermen for prey and have, therefore, been systematically culled on a large scale (IUCN 1981). In Norway, coastal killer whales were thought to be preventing recovery of an important stock of herring (*Clupea harengus*), so at least 327 whales were culled during the period 1978-1980 (IWC 1980, 1981, 1982). At Iki Island, Japan, fishermen became convinced in the 1960s that dolphins and small whales were eating, damaging, or scaring away most of the yellowtail (*Seriola* sp.) and squid on which the local fishery depended, so a massive program of government-supported culls ensued. The peak years of the control program were 1976-1980, when 934, 1332, 1646, and 1819 small cetaceans were killed, respectively; the species involved were *Tursiops truncatus*, *Pseudorca crassidens*, *Lagenorhynchus obliquidens*, and *Grampus griseus* (Kasuya 1985).

In Norway, the action was taken based on a general perception of adverse impact by the cetaceans, rather than on quantitative assessments. A later modeling study was "unable to find any combination of initial size, growth rate, and predation rate of the local killer whale population which could allow a take of a few hundred whales per year to be justified as expediting the recovery of the herring" (IUCN 1981). In the case of Iki Island, the cetaceans were undeniably interfering with the operations of the fisheries (stealing catches and scaring away fish and squid), but as yet there is no scientific basis for supposing any significant dynamic interactions between cetacean and fish or squid populations; the falling catch-per-effort in the fisheries could well be caused by overfishing (IUCN 1981), a problem for many of the Japanese home-island fisheries. In any case, the culls in both Norway and Japan were precipitated by falling fish catches, and thus it is likely that, whether or not cetaceans really are competitors with man for fishery resources to a significant degree (and they could be), many more such perceived conflicts will arise as human populations increase and fishery resources decline.

Habitat Loss and Degradation

Riverine habitats are highly vulnerable, and the great declines in many river dolphin populations can be attributed mainly to impingement by human activities other than hunting or fishing (Perrin and Brownell in press). Construction of dams and barrages on the Indus River and its tributaries has divided the population of Indus river dolphins into many small fragments, some of which have disappeared, perhaps because of disruption of their food supplies (Khan and Niazi in press). The same thing is happening to the Ganges river dolphin in Nepal (Shrestha in press) and India (Mohan in press) and may happen to the boto in Brazil if planned developments proceed (Best and da Silva in press). Dams and other water impoundments along the Yangtze River may have affected the supplies of fish that sustain the baiji, of which probably less than 400 remain (Chen and Hua in press). Another detrimental factor is the substantial and growing boat traffic on the rivers in developing nations that support populations of dolphins; for example, several baiji are thought to die annually in collisions with vessels on the Yangtze. Rivers are also extremely vulnerable to pollution by industrial effluent and agricultural runoff. Pollution is thought to be a major problem for the Ganges river dolphin in India (Mohan in press).

Coastal marine habitats as well as riverine habitats can be damaged by development and pollution, and populations of the cetaceans that are found only in shallow coastal waters or must migrate through them (e.g., *Sousa chinensis*, *Sousa teuszii*, *Neophocaena phocaenoides*, *Orcaella brevirostris*, *Eschrichtius robustus*, *Balaena mysticetus*, *Eubalaena* spp., *Megaptera novaeangliae*) can be put at risk by this degradation. For example, if petroleum exploration and development were to be allowed in the breeding lagoons of the gray whale in Mexico, the single remaining viable population of the species could be endangered. Even the high seas are not immune; plastic debris (including lost, or "ghost" fishing nets) may be responsible for the continuing decline of the Pribilof Islands fur seal herd (Fowler 1985) and could be entangling or otherwise affecting cetaceans as well.



The pantropical spotted dolphin *(Stenella attenuata)* is captured incidentally in tuna purse seines in large numbers in the eastern tropical Pacific. (Photo by W. High, courtesy of U.S. National Marine Fisheries Service)

Status of the Species and Populations

The Species

The cetacean species considered by the IUCN to be threatened are included in the Red List (IUCN 1988) under several categories:

Endangered: In danger of extinction, survival unlikely if causal factors continue operating. Includes taxa whose numbers have been reduced to a critical level or whose habitats have been so drastically reduced that they are deemed to be in immediate danger of extinction. Also included are taxa that are possibly already extinct but have definitely been seen in the wild in the past 50 years.

Vulnerable: Taxa believed likely to move into the Endangered category in the near future if the causal factors continue operating. Included are taxa of which most or all of the populations are decreasing because of overexploitation, extensive destruction of habitat or other environmental disturbance; taxa with populations that have been seriously depleted and whose ultimate security has not yet been assured and taxa with populations that are still abundant but are under threat from severe adverse factors throughout their range.

Insufficiently Known: Taxa that are suspected but not definitely known to belong to any of the above categories, because of lack of information.

There are three additional available categories not currently applied to any cetacean species:

Rare: Taxa with small world populations that are not at present Endangered or Vulnerable but are at risk. These taxa are usually localized within restricted geographical areas or habitats or are thinly scattered over a more extensive range.

Indeterminate: Taxa known to be Endangered, Vulnerable, or Rare, but where there is not enough information to say which of the three categories is appropriate.

Out of Danger: Taxa formerly included in one of the above categories, but which are now considered relatively secure because effective conservation measures have been taken or the previous threat to their survival has been removed.

In addition to the standard categories, the additional category of Not Threatened* has recently been developed for cetaceans (M. Klinowska, in litt.). These are taxa not at present sufficiently threatened to be included in one of the above categories but which are likely to qualify if the causal factors continue operating.

The Red List (IUCN 1988) status for each threatened cetacean species is given in Table 2; the non-threatened species are listed in Table 3. Summary accounts for status all the species will be given in a new Red Data Book under development (M. Klinowska, in litt.); the status of some species is under review, and their classifications may change.

Populations at Risk for Non-threatened Species

For many cetacean species that are not threatened with extinction or likely to be (Red List categories Endangered, Vulnerable, or Insufficiently Known), one or more populations are extinct, severely depleted, or currently under heavy pressure. For example, the striped dolphin inhabits warm-temperate and tropical waters around the world and is in no danger of extinction as a species, but the population that passes annually through the coastal waters of Japan has probably been overexploited in recent years and may have declined (IWC 1983a, Kasuya 1985). This action plan includes consideration of such threatened populations as well as entire threatened species. The inclusion of populations for the small cetaceans in the following summary list of populations at risk is conservative, i.e., if a population has been considered in recent years to be at least possibly at risk, it is included. For the whales that have been managed in the IWC (indicated with asterisk), all management units classified as Protection Stocks are included, with the exception of the stocks of *Caperea marginata*, for which there is no evidence of significant present or past exploitation (IWC 1987a). The list is, of course, provisional, as many situations involving directed or incidental exploitation of cetaceans are dynamic and volatile. It is certainly not comprehensive; new cases needing attention will continue to come to light.

Phocoena spinipinnis--Populations in Peruvian coastal waters (Gaskin et al. 1987)

Neophocaena phocaenoides—Yangtze and Chinese coastal populations (Wang 1984b)

Phocoenoides dalli—Western-central North Pacific, Bering Sea, and Japanese coastal populations (IWC 1984, Jones et al. 1987, Breiwick 1987, Miyashita and Kasuya 1987)

Sousa chinensis—All populations (of unknown but probably small size and highly susceptible to habitat degradation, e.g., in South African waters—Ross et al. 1987)

Sousa teuszii—All populations (small and highly susceptible to habitat encroachment--Maigret 1980)

Sotalia fluviatilis—Riverine populations in Brazil (da Silva and Best 1984)

Lagenorhynchus obscurus—Peruvian population (Gaskin et al. 1987)

Table 2. List of threatened cetacean species (IUCN 1988).

Endangered

Platanista minor	Indus river dolphin
Lipotes vexillifer	baiji, Yangtze river dolphin
Balaenoptera musculus	blue whale
Megaptera novaeangliae	humpback whale
Balaena mysticetus	bowhead
Eubalaena glacialis	northern right whale

Vulnerable

Platanista gangetica	Ganges river dolphin, Ganges susu
Inia geoffrensis	boto, Amazon river dolphin
Phocoena sinus	vaquita
Hyperoodon ampullatus	northern bottlenose whale
Eubalaena australis	southern right whale
Balaenoptera physalus	fin whale

Insufficently Known

Pontoporia blainvillei	franciscana, La Plata dolphin
Orcaella brevirostris	Irrawaddy dolphin
Delphinapterus leucas	white whale, beluga
Monodon monoceros	narwhal
Phocoena phocoena	harbor porpoise
Cephalorhynchus spp.	(4)

The baiji, or Yangtze river dolphin *(Lipotes vexillifer)*, is the most endangered cetacean; only about 300 remain. (Photo by Zhou Kaiya)

Table 3. List of non-threatened species. See text for explanation of Not Threatened* category.

Not Threatened*

Phocoena spinipinnis	Burmeister's porpoise
Neophocaena phocaenoides	finless porpoise
Australophocaena dioptrica	spectacled porpoise
Phocoenoides dalli	Dall's porpoise
Sousa chinensis	Indopacific hump-backed dolphin
Sousa teuszii	Atlantic hump-backed dolphin
Sotalia fluviatilis	tucuxi
Lagenorhynchus obscurus	dusky dolphin
Lagenorhynchus australis	Peale's dolphin
Tursiops truncatus	bottlenose dolphin
Stenella attenuata	pantropical spotted dolphin
Stenella longirostris	spinner dolphin
Stenella coeruleoalba	striped dolphin
Eschrichtius robustus	gray whale

Not Threatened

Steno bredanensis	rough-toothed dolphin
Lagenorhynchus albirostris	white-beaked dolphin
Lagenorhynchus acutus	Atlantic white-sided dolphin
Lagenorhynchus obliquidens	Pacific white-sided dolphin
Lagenorhynchus cruciger	hourglass dolphin
Grampus griseus	Risso's dolphin
Stenella frontalis	Atlantic spotted dolphin
Stenella clymene	clymene dolphin
Delphinus delphis	common dolphin
Lagenodelphis hosei	Fraser's dolphin
Lissodelphis borealis	northern right whale dolphin
Lissodelphis peronii	southern right whale dolphin
Peponocephala electra	melon-headed whale
Feresa attenuata	pygmy killer whale
Pseudorca crassidens	false killer whale
Orcinus orca	killer whale
Globicephala melas	long-finned pilot whale
Globicephala macrorhynchus	short-finned pilot whale
Tasmacetus shepherdi	Shepherd's beaked whale
Berardius bairdii	Baird's beaked whale
Berardius arnuxii	Arnoux's beaked whale
Mesoplodon spp.	(12)
Ziphius cavirostris	Cuvier's beaked whale
Hyperoodon planifrons	southern bottlenose whale
Physeter macrocephalus	sperm whale
Kogia breviceps	pygmy sperm whale
Kogia simus	dwarf sperm whale
Caperea marginata	pygmy right whale
Balaenoptera borealis	sei whale
Balaenoptera edeni	Bryde's whale
Balaenoptera acutorostrata	minke whale

Lagenorhynchus australis—Population in waters of Chile (Cárdenas et al. 1987) and Argentina (Goodall and Cameron 1980)

Grampus griseus—Populations in the Indian Ocean, e.g., off Sri Lanka (Alling 1985, Kruse et al. 1987)

Tursiops truncatus—Black Sea population (IWC 1983a), population off Natal, South Africa (Ross et al. 1987), populations off Peru (Gaskin et al. 1987), and likely others

Stenella attenuata—"Northern offshore stock" in eastern tropical Pacific (Smith 1983, Buckland and Anganuzzi 1987, IWC 1988), populations in coastal waters of Indian Ocean (Alling 1985, Kruse et al. 1987)

Stenella longirostris—"eastern stock" and "northern whitebelly stock" in eastern tropical Pacific (Smith 1983, Buckland and Anganuzzi 1987, IWC 1988), populations in coastal waters of Indian Ocean, e.g., off Sri Lanka (Alling 1985)

Stenella coeruleoalba—Population passing through waters of Japan during annual migration (IWC 1983a), populations in the Indian Ocean (Alling 1985, Kruse et al. 1987)

Delphinus delphis—Black Sea population (IWC 1983a), northeastern Mediterranean population(s) (Aguilar 1986), coastal populations in eastern tropical Pacific (Hall and Boyer 1987, Buckland and Anganuzzi 1987)

Globicephala melas—North Atlantic population(s) (exploited at Faroes, but status unknown—IWC 1987b)

Globicephala macrorhynchus—Population in northern Japanese waters (IWC 1987b)

Berardius bairdii—Western Pacific population(s) (exploited but status unknown—IWC 1986)

*Physeter macrocephalus**—North Pacific stock (western division) (Note: the status of this and other stocks around the world has been the subject of much scientific controversy within the IWC; e.g., see IWC 1983b).

*Eschrichtius robustus**—Western [Pacific] stock

*Balaenoptera acutorostrata**—Sea of Japan/Yellow Sea/East China Sea stock, West Greenland stock, West Norway/Faroe Islands stock

*Balaenoptera borealis**—All southern hemisphere stocks, all North Pacific stocks, Nova Scotia stock

*Balaenoptera edeni**—East China Sea stock

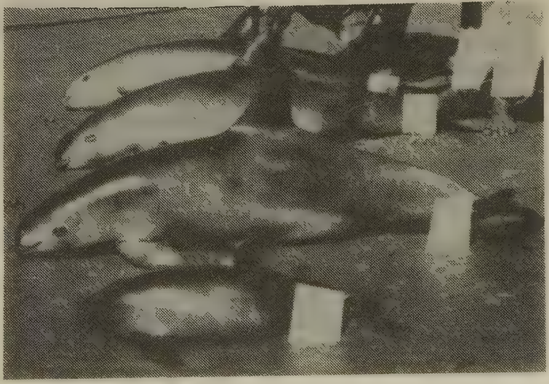
Recommended Conservation Action

Specific Projects and Actions

The following is a list of projects that the Cetacean Specialist Group believes should have priority for initiation or assistance. The brief explanatory comments are only meant to introduce the projects; fuller proposals or more details can be obtained from members of the Group (Appendix 1) or from research entities, governmental agencies, or conservation organizations in the region involved (Appendix 2). In many cases the cost estimates are rough initial approximations only—no detailed budgets have yet been compiled—but full proposals are being prepared and will be available on request.

There is an emphasis in these projects on regional, national, and local planning and participation in research and conservation activism; this is of course necessary if conservation and management of cetaceans is ever to be carried out on a continuing basis in the developing nations where most of the problems of survival of species and populations occur.

Several projects are of the very highest priority, clearly relating to risk of imminent extinction of species or populations. These are indicated with asterisks (*).



The vaquita or Gulf of California harbor porpoise *(Phocoena sinus)* has the most limited distribution of any cetacean species, being limited to the upper Gulf of California. Incidental takes in gillnets set for sharks and fish are a threat to the species. (Photo by A. Robles)

North America

1.* Monitor incidental catches of vaquita in Gulf of California, Mexico $20,000

The vaquita or Gulf of California harbor porpoise, *Phocoena sinus*, is endemic to the upper Gulf of California. Large numbers have been killed in gillnet fisheries, and the species' status is uncertain; it is rare and thought to be vulnerable because of its limited range (Barlow 1987). A census survey is in progress (in 1987), but field surveys and monitoring are needed to determine the rates of incidental kill in all gillnet fisheries within the range. A report on the problem will be submitted to the Mexican government, with recommendations for fishery management actions and an educational program to increase lay awareness of the uniqueness of this endemic Mexican species and the threats to its survival. The cost estimate is for one year of fieldwork and data collation and preparation of the report.

South America

2.* Reduce illegal use of small cetaceans for crab bait in South America $50,000

Several thousand dolphins and porpoises are harpooned annually for use as bait in the Chilean crab fishery, along with fur seals, sea lions, penguins, guanacos, and other wildlife (Leatherwood et al. 1984, Cárdenas et al. 1986, 1987). The abundance of at least one dolphin, *Cephalorhynchus commersonii*, may have been drastically reduced. Other species involved are *Lagenorhynchus australis*, *L. obscurus*, *Cephalorhynchus eutropia*, and *Phocoena spinipinnis*. Only 4 of 26 crab companies operating in the Magallanes area provide bait to the crab fishermen, and even in those cases the amount supplied is grossly inadequate. The crab fishery is expanding rapidly and now extends to the area south of the Beagle Channel, which is being fished extremely heavily at present. The multimillion-dollar catch is exported to the U.S.A., Germany, France, Holland, Belgium (a re-exporter), Japan, and Italy. The fishery operates freely in an illegal mode because of isolation of the area and non-enforcement of national laws. Funds are needed to develop national and international information campaigns to inform the citizenry, environmental organizations, and the governments of the importing nations of the illegal nature and the serious environmental effects of the crab fishery. Support is also needed for the development of cetacean research projects in the area that involve the authorities, universities, NGOs, and liaison with similar programs and governmental agencies in Argentina, so as to establish a strong scientific presence in the region to foster local awareness of the importance of resource conservation and observance of wildlife laws. This program will also provide training for local and national researchers. Emphasis in the research will be on collection of more definitive statistics on bait usage, on survey of the marine mammal populations affected and on development of alternative sources of bait.

3. Continue work on fishery interactions and direct exploitation in Peru $20,000

A survey conducted in 1984-1986 showed that a wide variety of small cetaceans is taken incidentally in gillnets and deliberately in seines and by harpoon and landed at several fishing ports in Peru for human consumption (Gaskin et al. 1987). The major species involved are *Lagenorhynchus obscurus*, *Phocoena spinipinnis*, *Delphinus delphis*, *Tursiops truncatus*, and a pilot whale (*Globicephala macrorhynchus* or *G. melas*). More than 500 small cetaceans were landed at one small port during a period of about 200 days, and the total catch may approach 10,000 in some years. The impacts of this on the cetacean populations are unknown; the numbers taken of *L. obscurus* in particular is of concern. The official catch statistics presently collected are accurate, but do not break the catch down by species or number. Further funding is needed to produce training materials and conduct training sessions in species identification and the collection of dolphin-fishing effort data for the fishery officials who monitor the catches at the major ports. Planning should also begin for research to assess the status of the population(s) of *L. obscurus* and to address the possible need for regulation of the directed fishery for that species. Collection of biological samples from carcasses landed at several ports should continue, to provide baseline data which could be used to detect changes in reproductive parameters, body condition, or feeding habits related to exploitation and/or large-scale environmental changes such as occurred during the recent major El Niño event. The cost estimate is for the training program and for one year of continued sampling of the landings.

4. Conduct survey of coastal fishery interactions in Brazil $30,000

Small cetaceans are killed incidentally in gillnets and seines and harpooned in many places along the central and northern coasts of Brazil (unpublished information from Fundação Brasileira Para a Conservação da Natureza). They are used for shark bait, for human consumption, and as a source of "love charms." *Sotalia fluviatilis* is known to be taken (Anon. 1985), but the degree of involvement of other species and the size of the kill are unknown. Preliminary data exist on the incidental kill and direct take of *Tursiops truncatus*, *Sotalia fluviatilis*, and *Pontoporia blainvillei* in southern Brazil (Anon. 1985, Praderi et al. in press), but more precise information is needed, particularly for the first two species. Preliminary surveys to identify landing ports and collect data on the size and species composition of the catches in northern and central Brazil are badly needed, and the survey work begun in southern Brazil should be expanded to collect additional data on species composition, size, seasonality, value, and utilization of the catches. The surveys would best be conducted in three parts: 1) northern Brazil from Belem to Salvador (Bahia) (major ports are Belem, São Luis, Parnaiba, Fortaleza, Natal, João Pessoa, Recife, Maceio, and Sergipe), 2) central Brazil from Salvador to São Paulo (Salvador, Ilheus, Vitoria, Macae, Niteroi, Rio de Janeiro, Santos, and other, smaller ports), and 3) southern Brazil (Paranaguá, São Francisco do Sul, Itajaí, Florianópolis, Laguna, and Tôrres). The southern effort should be coupled with northward expansion of the existing stranding salvage program at Rio Grande Sul. This project would coordinate with an existing WWF-funded project by FBCN-GMA to monitor incidental catches of *Pontoporia blainvillei* in the Rio de Janeiro region and a national marine mammal stranding/salvage network presently being organized.

5. Continue monitoring of incidental kill of franciscanas in Uruguay $15,000

The incidental take of *Pontoporia blainvillei* in Uruguayan coastal fisheries has been well documented and is presently at a relatively low level (Praderi et al. in press), but the situation needs monitoring on a continuing basis because of possible changes in operations or intensity of the shark gillnet fishery. In addition, the incidental catch should be monitored closely to detect any changes in age or sex composition, or in reproductive parameters. The ecological relationships between the dolphins and the exploited fishes and sharks should also be examined, as well as the mechanics of the incidental kill and possible solutions. Data should also be collected on other dolphins taken in the fishery. This project would coordinate with an existing similar effort in Brazil (No. 4 above). Funds are needed for field subsistence, supplies, and equipment, for purchase of incidentally killed dolphins, and for extraction of fishery statistics.

6. Improve statistics on fishery interactions in Argentina $20,000

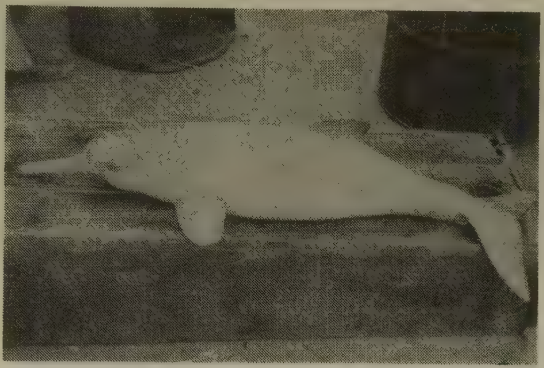
At least several hundred franciscanas, *Pontoporia blainvillei*, and unknown numbers of dolphins of other species are killed annually in gillnet fisheries in northern Argentina, but the data for several important ports are lacking or incomplete (Pérez Macri and Crespo in press). Along the central coast, *Globicephala melas* and *Tursiops truncatus* are known to be taken in trawl nets (Bastida and Lichtschein 1986), but the available data are fragmentary. In southern Argentina, *Cephalorhynchus commersonii*, *Phocoena spinipinnis*, and *Lagenorhynchus australis* are taken incidentally in crab nets and harpooned for crab bait (Goodall and Cameron 1980, Anon. 1985). The collection of kill statistics in both areas needs to be expanded and regularized and the impacts on the populations of small cetaceans assessed. This would most efficiently be done by division of the coastline into zones corresponding to the major fishery areas: 1) the coast north of Buenos Aires, 2) the Buenos Aires region, 3) northern Patagonia, and 4) southern Patagonia including Tierra del Fuego (where cetaceans are taken for crab-bait as in Chile (see No. 2 above); the subprograms would be based at universities and other institutions in the respective areas and would coordinate their activities closely. Funds are needed for an organizational meeting to develop a national research plan, for subsistence, for fuel and other supplies, and equipment for field work, and for collation and publication of data, technical reports, and reports to government agencies to recommend management actions.

7. Assess right whale habitat in Argentina $5,000

The region surrounding the breeding habitat of the southern right whale, *Eubalaena australis*, near Peninsula Valdes in Argentina is undergoing rapid industrial development (Bastida et al. 1985). Commercial fishing in the area is increasing, and exploration for petroleum is likely to occur in the near future. An evaluation of the necessary extent of a breeding sanctuary and the probable impacts of the new developments is badly needed. The report of this evaluation will go to the Argentine agency responsible for establishment and management of wildlife reserves and to the agencies responsible for petroleum development.

8. Promote regional plan to coordinate research on franciscana in Brazil, Uruguay, and Argentina $5,000

The franciscanas involved in gillnet fisheries in Brazil, Uruguay, and Argentina may belong to a single large population or may consist of two or more populations (Perrin and Brownell in press). There may be seasonal north-south migrations. Investigators in government agencies and other institutions in the three countries should meet to draft a cooperative plan for coordinated research, to maximize the cost efficiency of the research and to give attention to possible cross-boundary migration and fishery effects.



The franciscana *(Pontoporia blainvillei)* is one of the smallest cetaceans; adults may be less than 1.3 m long and weigh less than 30 kg. (Photo by R. Praderi)

9. Design survey to estimate population size of franciscana $10,000

There is no estimate of abundance and it is not known how many populations exist. The probable incidental gillnet kill of tens of thousands over the last 30 years may have had a significant impact on the population(s) (Praderi et al. in press). Key researchers in Uruguay, Brazil, and Argentina should consult to select a survey method and site, and a pilot survey to establish feasibility and lay a basis for estimating overall costs should begin as soon as possible. This should be coupled with stranding surveys to determine seasonal changes in total range. Following the pilot survey, plans should be developed for a larger-scale comprehensive survey perhaps involving the territories and resources of more than one nation. The results of the survey, in combination with improved estimates of incidental kill (see 4, 5, and 6 above) will form the basis for recommendations for management action. The cost estimate is for the initial consultations, the pilot survey and the subsequent development of the overall survey plan.

10. Monitor incidental kill of dolphins in Amazon fisheries in Brazil $25,000

Both *Inia geoffrensis* and *Sotalia fluviatilis* are killed incidentally in fisheries on the Amazon and its tributaries, and dolphin parts enter trade for use as love charms (Best and da Silva in press). Statistics collected to date are fragmentary. A minimum two-year pilot program to collect comprehensive data on incidental kills should be designed and started. The project should be headquartered at INPA in Manaus, where the previous work has been done, and utilize field surveys at all of the significant fishing ports on the river. The field program should include collection of specimens and data from carcasses for studies of the reproductive capacity of the populations. At the end of two years, the results should be evaluated to determine if monitoring must continue on a permanent basis.

11. Promote establishment of river dolphin conservation areas in Brazil $15,000

Development of the Amazon basin is proceeding rapidly, and riverbank deforestation, construction of hydroelectric dams, commercial fishing, and other activities are leading to massive degradation and loss of habitat essential to populations of river dolphins and other components of the riverine fauna such as manatees, crocodiles, turtles, endemic fishes, and aquatic birds (Best and da Silva in press). While there is still time, areas of prime aquatic habitat containing large numbers of river dolphins should be identified and be given protection as conservation areas in which the perturbing and destructive activities are prohibited or their impacts substantially minimized. The first step will be to prepare an inventory and prioritization of habitat areas. Some field survey may be required. The inventory and recommendations for designation and management of habitat reserve areas will be submitted to the appropriate Brazilian agencies and will be published for broader dissemination.

12. Promote legislation to fully protect river dolphins in Peru, Ecuador, Colombia, and Venezuela $5,000

River dolphins (*Inia geoffrensis*) are explicitly protected in Brazil and Bolivia but have no protection, only partial protection, or are of uncertain status in the other countries including parts of the basins of the Amazon and Orinoco (Atkins in press). A thorough inventory of existing wildlife protection laws and regulations in these countries and an analysis of the adequacy of these legal measures given the known threats to river dolphins is needed, so that detailed recommendations and justifications can be prepared and given to the appropriate government agencies.

13. Promote enforcement of existing laws protecting river dolphins in South America $8,000

Existing laws fully protect river dolphins in Brazil and Bolivia, and the dolphins are partially or implicitly protected by wildlife laws in Peru, Colombia, and Venezuela (Atkins in press). Enforcement of the relevant laws and regulations is not adequate because of shortages of resources, including patrol boats, enforcement agents, and field posts. Direct funding is required to recruit and train enforcement agents, purchase or refurbish patrol boats, construct or purchase field facilities, and provision field patrols. The first step would be to request information and preproposals from the respective national wildlife agencies and to develop a logistical plan and comprehensive proposal; the cost estimate is for this initial phase.

14. Establish dialogue on river dolphin conservation and management among Brazil, Peru, Venezuela, Colombia, Ecuador, and Bolivia $10,000

The river basins that comprise dolphin habitat extend to all of these countries, and in some cases it is clear that dolphin populations are likely also shared (Best and da Silva in press). The goal in consultations and discussion among the countries should be to develop coordinated regional approaches to conservation of the riverine habitats and faunas. The first step would be a consultative meeting of scientists working with river dolphins in South America and representatives of the national wildlife and development agencies. The immediate goal would be to establish an ad hoc regional liaison committee and draft lists of concerns and recommendations. Possible umbrellas for this include the IUCN and the Treaty for Amazonian Cooperation, to which all of the nations involved are parties. Possible national cooperating groups are listed in Appendix 2.

Europe

15. Assess status of common dolphin in western Mediterranean $20,000

The western Mediterranean population of *Delphinus delphis* seems to have declined precipitously in recent years. Museum records show that the common dolphin was an abundant species in the northern basin up to the early 1970s, but it has since become extremely rare. Since 1978, there have been no strandings in northern Spain or in northern Italy, and only 7 of 238 cetaceans stranded on the Mediterranean coast of France were of this species (Aguilar 1986). The species continues to be abundant in the southern basin (Duguy et al. 1983). The cause of the apparent decline in unknown, but possible causes include pollution, overfishing of food resources, unregulated direct exploitation in Spain and indirect catches (known to exist but of unknown size) in Spain, France, and Italy. It has also been suggested that the common dolphin has been replaced by an expanding population of the striped dolphin (*Stenella coeruleoalba*). Aerial and/or boat surveys are needed to determine present distribution, estimate density, and examine possible interaction and overlapping of distributions of the two species. Likely sources of mortality should be identified more clearly, and, if possible, quantified. Questions of stock identity (especially between Mediterranean and Atlantic populations) should be investigated by means of tagging studies using artificial or natural marks and biochemical approaches. Because the common dolphin and striped dolphin have been confused in the past (e.g., Richard 1936), a thorough review of existing data and specimens in Spain, Portugal, France, and Italy should be carried out. If human-related causes are implicated in change in abundance of the dolphin, appropriate recommendations for feasible action will be submitted to the governments of the nations bordering the western Mediterranean. The cost estimate is for field and laboratory work to examine density, distribution, and stock identity off Spain and in the Strait of Gibraltar, evaluation of the magnitude of direct catches off southern Spain, and review of all existing material.

Africa

16. Assess populations of bottlenose dolphins in Natal, South Africa $10,000/yr for 3 yrs

Anti-shark nets off bathing beaches may have removed as much as 30-34% of the local population of bottlenose dolphins (the long-beaked "aduncus" form of *Tursiops truncatus*) off southern Natal during the period 1980-1985 (Ross et al. 1987).

The Indo-Pacific humpbacked dolphin, *Sousa chinensis*, is also involved. Aerial surveys have not proved effective because of water turbidity. A census based on individual-animal recognition is needed urgently, to allow assessment of the status of the population and estimate impact of the nets with more confidence.

17. Review incidental kills and direct exploitation of small cetaceans in West Africa $40,000

There is a long history of subsistence take and incidental kill of small cetaceans in coastal fisheries of several West African nations (Cadenat 1959, Maigret 1980, 1981), but there has been no survey of the fisheries since the widespread introduction of monofilament gillnets. Large pelagic trawlers fishing the continental shelf also capture some small cetaceans. The species involved include *Delphinus delphis, Tursiops truncatus, Stenella attenuata, Stenella longirostris, Stenella frontalis, Stenella clymene, Steno bredanensis, Sousa teuszii, Kogia* sp., and possibly others. The nations known to be involved are Mauritania, Senegal, and the Ivory Coast; others likely have similar coastal fisheries and catches of cetaceans. A preliminary survey of the coastal fisheries in all of the West African nations is badly needed. This would be carried out in close collaboration with the respective national fishery services, which routinely collect fishery data through local contacts and agents. Funds are needed to commission the collection of additional information by the national agencies and to support an investigator to visit the nations involved and to collate and report the findings. The products will include reports to the appropriate governmental agencies of nations where potentially significant fishery interactions are identified, with recommendations for management action.

Asia and Australasia

18. Estimate catches and status of populations of dolphins in Taiwan $14,000

Tursiops truncatus and dolphins of other species are captured in a drive fishery and other fisheries in Taiwan and sold for human consumption within the country (Wang 1984a). The bottlenose dolphins are of the long-beaked tropical "aduncus" variety of the species (see Ross 1984). At present the catches are not monitored, and the distribution, size, and status of the dolphin populations are unknown. A catch monitoring and sampling program needs to be established, and research to assess the bottlenose dolphin population should begin. The cost estimate is for first-year costs of the catch-monitoring program only. Four years of research on samples collected from the fishery would cost approximately $40,000. The cost of aerial or ship surveys to census the population would depend on the survey platform chosen and the geographical extent of the surveys but would likely be less than $100,000. Should this pilot study reveal a likely significant level of fishery take, the products will include recommendations to the Government of Taiwan for a broader investigation and/or management action.

19. Monitor incidental gillnet catches in Sri Lanka $25,000

Many thousands of dolphins die annually in coastal gillnet fisheries in Sri Lanka (Alling 1985). The primary species are *Stenella longirostris, Stenella coeruleoalba, Stenella attenuata*, and *Grampus griseus*. A preliminary survey of the principal ports has been carried out; the need now is for a network of observers to monitor the catches on a continuing basis, so that seasonal and regional variation can be accounted for in estimating total catches and in later assessment of the dolphin populations and the impacts of the catches. An ultimate goal of the program will be to develop recommendations for management actions such as seasonal or area closures to minimize the fishery impacts on the cetacean populations. Funds are needed to train village people to collect data in fisheries in their areas, to set up a system to gather the information in a central location, and to analyze the data and publish the results.

Bottlenose dolphins *(Tursiops truncatus)* are captured for human consumption in coastal waters of Taiwan. (Photo by N. C. H. Lo)

20. Monitor incidental gillnet catches in India $20,000

Large numbers of dolphins are killed in Indian coastal gillnet fisheries (Mohan 1985). The meat is consumed locally. *Stenella longirostris* and *Tursiops truncatus* are the principal species. The size and status of the populations are unknown. The Central Marine Fisheries Institute in Calicut has recently established a system for collection of data on incidental catches, using personnel already sampling the fish catches. The monitoring centers are at Veraval, Bombay, Goa, Mangalore, Calicut, Cochin, Trivandrum, the Cape, Mandapam Camp, Madras, Kakinada, Waltair, Puri, and Calcutta. The monitoring centers will also collect information on stranded cetaceans, including evidence of fishery involvement. Incidental catches, strandings, and sightings will be used to determine ranges of the species and populations in Indian waters. Funds are needed to train the samplers in cetacean identification and determination of sex, length, and reproductive condition, and to support collation and analysis of the data and publication of the results, including possible recommendations for management actions to ameliorate identified critical problems.

21. Examine status of dwarf spinner dolphin in Thailand $5,000

A dwarf form of *Stenella longirostris* has recently been discovered in the Gulf of Thailand (Perrin et al. 1987b). The range of the population may be limited and total abundance small. Carcasses are unloaded by fishing vessels at Bangkok and sold locally for human consumption. It is not known if these are captured intentionally or incidentally, nor are the size or the exact location of the catches known. Funds are needed for locally-based monitoring of the landings and for research into their source. Should the levels of incidental take prove potentially significant, a broader program of research to estimate the fishery impact and develop management recommendations will be designed.

22.* Census populations of Ganges river dolphin in India $30,000

No complete census of river dolphins, *Platanista gangetica*, has been carried out in India. It is thought that populations there are declining rapidly, primarily due to habitat degradation (Mohan in press), and it is very important that a baseline census be carried out so that trends can be monitored. It is especially important that the Brahmaputra River be surveyed in detail. Efforts will be made to standardize survey techniques with those used in other censuses of the species in Bangladesh and Nepal, so that results can be combined and compared. Funds are needed for training, support, and transportation of census personnel, and for hire of river vessels. The results of these studies and those of similar census efforts proposed for other parts of the range of the species (Nos. 26 and 27 below) will feed into the initiatives to establish reserves (Nos. 24 and 28) and develop regional approaches to assessment and conservation of the species (Nos. 30 and 31).

23. Develop alternative to use of dolphin oil as fish lure in India $10,000

The directed fishery for the Ganges river dolphin in India can be slowed or stopped if an inexpensive and readily available substitute can be found for the dolphin oil used by fishermen to lure catfish into their nets (Mohan in press). Biochemical analysis is needed to determine the active principle in the oil, and technological research is needed to test alternate substances in laboratory and field conditions.

24. Promote establishment of dolphin sanctuaries in the Brahmaputra River in India $4,000

Ganges river dolphin habitat is rapidly being degraded in India (Mohan in press). Field surveys are needed to identify and inventory relatively intact stretches of prime habitat along the Brahmaputra River. The areas must be prioritized, and reports and recommendations directed to the agencies responsible for establishment of parks and reserves. This project would be carried out in conjunction with No. 22 above, the survey of population sizes. The cost estimate is for the preparation and publication of reports.

25. Investigate effects of dams on Ganges river dolphin in India $10,000

Draw-down of rivers, in particular, is thought to have had serious adverse effects on dolphin habitat and population size (Mohan in press). More impoundments and control projects are planned. Funding is needed to support field research on existing dams, impact assessment studies for planned dams and preparation of recommendations to governmental planning and development agencies.

26.* Census populations of Ganges river dolphin in Bangladesh $10,000

As in India, abundance of river dolphins in Bangladesh seems to be declining sharply (Aminul Haque in litt.) and the populations have not been adequately surveyed. Action is needed quickly to establish baseline population estimates. Funds are needed for training, support, and transportation of field personnel and for hire of river vessels.

27.* Census populations of Ganges river dolphin in Nepal $10,000

The two river systems surveyed to date contain less than 50 dolphins (Shrestha in press). Census surveys should be carried out on all of the rivers in Nepal containing or suspected to contain dolphins, and the populations should be monitored on a regular basis. Funds are needed for transportation and for hire of survey vessels.

28.* Inventory river dolphin habitat in Nepal and promote establishment of sanctuaries $4,000

Dolphin habitat in Nepal is different from that in India and Pakistan, involving deeper, clearer water and swifter currents, and is rapidly diminishing due primarily to hydroelectric development (Shrestha in press). The ecological characteristics of the dolphin habitat in the Karnali River (where a high dam is planned to be constructed in the near future) should be fully described and the likely future impacts of flood, drought, and oversilting evaluated. The information gained should be used to inventory prime areas of dolphin habitat throughout Nepal and identify those that are in danger from planned development and those that are the best candidates for dolphin sanctuaries. Funds are needed for field survey and preparation of reports and recommendations.

29. Reduce medicinal use of dolphin oil in Nepal $2,000

Dolphins are netted by Nepalese fishermen and marketed for their oil, which is used as a remedy for a wide variety of diseases (Shrestha in press). Support is needed for educational posters and lectures in the villages to inform local people of the endangered status of the dolphin and to suggest alternative and more efficacious medications.

30. Establish regional river dolphin research committee $5,000

A regional research committee with members from India, Bangladesh, Nepal, and Bhutan should be formed and meet in a central location to discuss research plans, standardize methods, and evaluate results. As this committee would be international, the IUCN or WWF would be suitable parent organizations. Funds would be required for transportation to committee meetings; the cost estimate is for the initial organizational meeting.

31. Establish IUCN river dolphin project $20,000

Focal centers of research on the Ganges river dolphin and its ecosystem should be established at major universities on the Ganges/Brahmaputra River systems. These would include Gauhati University on the Brahmaputra and Benares University on the Ganges in India, Chittagong University on the Karnaphuli and Mymensingh University on the Ganges in Bangladesh, Tribuhwan University in Nepal, and Thimphu University in Bhutan. Initial steps would include correspondence with professors to acquaint them with the important research and conservation problems that must be addressed for this species and placement of books, reports, and reprints in university libraries. Attempts would be made to initiate projects on reproductive biology and behavior, ecology, population dynamics and movements, in addition to the higher-priority projects identified in the Action Plan. Funds would be solicited and activities coordinated under an umbrella River Dolphin Project similar to the highly successful Tiger Project. The cost estimate is for the first two years of operation, including purchase and posting of reference materials and several very small "seed-money" research stipends. A heavy emphasis would be placed on developing recommendations to governments for conservation and management actions. The project could also serve as a base of coordination for the regional research review committee (No. 30 above).

32.* Reverse decline of Indus river dolphin in Punjab $83,000

Only about 500 Indus dolphins remain (Khan and Niazi in press). Most of these (over 400) are in the dolphin reserve between the Guddu and Sukkur barrages in the Sind, where they are well protected. The situation in the Pakistan Punjab is critical; only 62-72 survive in the thousands of km of habitat above the Guddu Barrage in the Punjab in four isolated and unprotected populations, and monitoring surveys indicate that these populations are declining rapidly. Other populations known to have existed in the past in the region have disappeared. Field research is urgently needed to determine and quantify the cause(s) of mortality and to project the future course of the populations. It is likely that the establishment of one or more reserves and enforcement of legal bans on hunting by the governments of Pakistan and the Punjab will be needed if the species is not to become extinct in the Punjab and its overall range in Pakistan to shrink to a very small portion of its original size. In addition to bans on killing dolphins, a prohibition is needed on possession, sale or purchase of dolphin meat, oil, or bones. Funding is needed for survey of potential reserve areas, preparation of reports and recommendations, hiring and training of enforcement agents, boats and vehicles for research and patrol, field subsistence, and education of the villagers. The budget estimate is for a two-year program.

33. Expand research on Indus river dolphin in Sind, Pakistan $30,000

In addition to continuing regular population censuses, research in Sind should concentrate on obtaining quantitative estimates of calf production and mortality and on determining limiting habitat parameters and precisely mapping and monitoring existing utilized and vacant habitat along the full length of the river. It is critical that it be determined whether the population is indeed increasing and what the future trend will likely be, so the recommendations can be made to the Sind Government for further management actions if necessary. Funding is needed for salaries, field surveys, equipment, supplies, laboratory work, and preparation of reports.

34.* Reduce kill of baiji in Yangtze River $100,000

Despite legal protection, significant numbers of dolphins are killed incidentally in fisheries and accidentally by vessels and by explosions during river bank construction (Chen and Hua in press). Every effort must be made to eliminate or reduce the use of the "rolling hook" fishing gear in the regions of high dolphin density and to develop procedures to ensure that dolphins are absent or removed from the area before high explosives are used in construction on the river. Regulations concerning vessel traffic in existing and proposed reserves must be enforced. At present, resources available to enforce existing legal protection are not adequate. Funding is needed for a patrol vessel for enforcing regulations in the reserves and elsewhere along the river.

35.* Complete baseline studies for baiji reserve at Shi Shou, China $35,000

Before dolphins can be placed in the proposed semi-natural reserve at Shi Shou, studies must be carried out on the probable effects of high-dam construction upriver, levels of contaminants in the water, bottom sediments and food fish, and seasonal changes in the quantity and nutritive quality of naturally occurring food fish. Funds are needed for hydrologic analyses, field surveys, and laboratory analyses.

36.* Continue monitoring baiji population $20,000/yr

Only a few hundred baiji remain; it is the most endangered cetacean (Chen and Hua in press). At present, resources are not available to continue the population monitoring that began in 1985 and 1986. It is critical that the monitoring continue, so that the trajectory of the population can be estimated, the effects of existing protection measures assessed and additional measures recommended. The survey lasts several weeks and requires the charter of small fishing vessels as well as the use of research vessels.

37.* Determine movements and population structure of baiji $63,000

The extent of movement of individual dolphins along the Yangtze is not known (Perrin and Brownell in press). This information is vital to population survey design and evaluation of results and to determine the degree of isolation of groups or subpopulations along the several thousand km of river. The results will be critical to evaluation of the effectiveness of existing and proposed reserves. Studies should begin immediately to

Several gray whales (*Eschrichtius robustus*) become entangled in coastal gillnets and die each year during seasonal migrations along the California coast. (Photo by S. Leatherwood) monitor movements; possible techniques include use of conventional tags, radio-tracking, and compilation of a catalog of individuals using natural marks. Funding is needed for consultation with researchers experienced in studying dolphin movements, for photographic equipment and film, for radiotags, and for logistical support of field research, including charter of several fishing vessels for capture operations.

38. Survey the status of cetaceans in Chinese waters $35,000

Very little is known about the marine cetacean fauna of China (Wang 1984a and b). A survey of coastal regions and fishing ports to determine the species present and document any involvement with fisheries is badly needed. A network of coastally located scientists, fishery officials, and other interested officials should be established to collect data on strandings and fishery catches. Creation of such a network will require availability of a Chinese-language guide to identification of cetaceans; such a guide does not exist and must be written and published. The cost estimate is for preparation of a guide, the initial establishment of the network and preparation of an interim report on fishery interactions to the appropriate governmental agencies.

39. Assess and reduce incidental kill of Hector's dolphin in New Zealand $20,000

Hector's dolphin, *Cephalorhynchus hectori*, is endemic to New Zealand coastal waters. A survey of distribution and abundance in 1984-1985 indicated a total population of only 3000-4000 (Dawson and Slooten in press a and b). Entanglement in gillnets (commercial and recreational) may be a threat to continued existence of the species; in an area for which data were collected, 10-15% of the population is estimated to be killed in nets annually (Slooten and Dawson in press). Better data are needed on kill rate and population size. Funds are also needed to develop management strategies (e.g., net modifications and/or fishing regulations).

Non-regional

40.* Convene workshop on gillnets and cetaceans $40,000

Many of the emerging problems of cetacean conservation involve coastal and pelagic gillnet fisheries. An international workshop meeting of national fishery experts and cetologists is needed to focus research and management efforts to define and ameliorate these problems. Emphases will be to identify gillnet fisheries that impact cetaceans, to design programs to collect adequate statistics on incidental kill and to discuss possible ways to reduce the incidental kills through technological research and innovative management. It will be especially important to involve participants from the developing nations that are placing high priority on coastal and offshore fishery development. Nations in which incidental kill in gillnets likely occurs but for which there is almost no information include Pakistan, Bangladesh, Indonesia, the Philippines, the Malagasy Republic, Papua New Guinea, Surinam, Brazil, Argentina, the French Antilles, Venezuela, Mozambique, Tanzania, Kenya, the Somali Republic, Burma, Thailand, Malaysia, Kampuchea, Vietnam, and many others. Participants should also be included from the nations where research and management programs have been developed to address the problem, such as the U.S., Japan, Canada, and Australia.

41. Resolve taxonomy and distribution of the humpbacked dolphins, *Sousa* spp. $8,000-10,000

Two species, the Indo-Pacific humpbacked dolphin, *S. chinensis*, and the Atlantic humpbacked dolphin, *S. teuszii*, are currently recognized by most cetologists Ross (1984), although some recognize a third, *S. plumbeus* (e.g., Zhou et al. 1980), or even a fourth, *S. lentiginosa*, and a fifth, *S. borneensis* (e.g., Pilleri and Gihr 1980). All are restricted to shallow coastal waters. Recent research indicates that it is possible that only a single species exists, with very greatly differentiated regional populations that differ in average coloration, size, shape, and skull characters (Ross 1984). These populations are presumably morphologically adapted to local ecological conditions. Because of the vulnerability of the local populations of these small coastal cetaceans to habitat degradation and direct and indirect exploitation, it is extremely important that the species structure of the group be critically examined, the regional populations identified and their ranges delineated. The problem is especially urgent in West Africa, where local populations may consist of less than 100 individuals (Maigret 1980). The undertaking will involve as a first phase the comprehensive examination of museum specimens, available photographs, and published and unpublished locality records. The cost of this first phase will depend on where the investigators are located. A second phase may include several field surveys to establish limits of distribution and delineate habitats (not included in cost estimate).

A third phase would include assessment of the status of the populations most at risk and development of recommendations for national management actions.

42.* Promote increased consideration of river faunas in internationally funded development $20,000

Planning for the protection of river dolphins and the associated aquatic fauna should be an integral part of regional planning for the entire river system or basin (Perrin and Brownell in press). In this planning, consideration of the dolphins should be part of a broad attempt to accommodate the needs of wildlife, fisheries, and economic development. International funding agencies should be informed of the vulnerable position of the river dolphins and be requested to use appropriate guidelines in environmental assessments. Funding is needed to commission preparation (through correspondence) of detailed draft guidelines to be recommended to the organizations, such as the World Bank, multinational corporations, and international joint ventures, presently engaged in or planning developments in major tropical river basins. These guidelines would not be meant to substitute for expert on-site consulting, but would serve to alert the planners to the issues.

43. Review effects of disturbance on coastal and riverine cetaceans $18,000

Rapidly increasing vessel traffic, mining, and petroleum developments and fishery activities are impinging progressively on the habitats of riverine and coastal dolphins, porpoises, and whales. Noise, physical intrusion, sea bottom destruction, and overall habitat alteration are the consequences of these developments. Their effects on behavior and migrations have been investigated for large whales, especially in relation to petroleum resource developments (Geraci and St. Aubin 1980, Stirling and Calvert 1983, Sorensen et al. 1984), but nearly nothing is known of effects on small cetaceans. Research indicates that reaction of cetaceans to specific human activities varies according to the species, type, and intensity of human activity, feeding habits of the species studied, and possibly other factors (Sorensen et al. 1984, Watkins 1986). Funding is needed to commission a review of existing knowledge on both small and large cetaceans and to organize a workshop meeting of experts (about 50 people for 5 days, in Europe) to identify cetaceans populations most likely to be affected and to draw up and prioritize recommendations for research.

44. Conduct workshop on population-census methods for coastal and riverine dolphins $25,000

Census methods for oceanic cetaceans are well-advanced; the line transect method is in wide use and yields accurate and adequately precise estimates for management. However, the line transect method is not entirely suitable or practicable for dolphins in a nearshore habitat or in a river, and none of the other methods in use are fully satisfactory either (Perrin and Brownell in press). A workshop meeting is needed to compare and critique the methods presently in use and develop improved approaches. It is very important that survey methods be improved and standardized so that the results of the several survey efforts proposed or in the offing be reliable and comparable.

Other Issues and Projects to be Monitored

Many national and international agencies and organizations are actively endeavoring to conserve and manage cetaceans. In some cases these efforts are successful; in others the outcome is still uncertain. In some situations of obvious potential for overexploitation, research to assess the populations is underway; in some other situations, there is no apparent immediate or long-term risk of extinction of populations under present circumstances. IUCN's strong support for the internationally agreed moratorium on commercial whaling (that theoretically took effect in 1986), has been made clear in its statements to the annual International Whaling Commission meetings over the last several years. IUCN regrets that even now the moratorium has not been completely implemented. Some issues, such as what should constitute whaling under scientific permit issued by parties to the International Convention on Whaling, are under intensive debate and may or may not be resolved during the term of this Action Plan. In addition to attempting to launch or assist the specific projects recommended above, the Cetacean Specialist Group will monitor these issues and situations and, if necessary, add projects to the Plan in line with developments. The Group endorses the research ongoing in relation to these issues and believes that it should continue. The list that follows is not exhaustive; items will be added as they come to the attention of the Group. Background information on nearly all of these topics can be found in Report of the International Whaling Commission, Volumes 30-38 (1980-1988).

North America and Greenland

1. Status of white whales exploited by native peoples in Alaska, Canada, and Greenland.
2. Status of white whales exploited in the USSR.
3. Status of narwhals exploited by native peoples in Canada and Greenland.
4. Incidental kill of harbor porpoise in the Bay of Fundy, Canada.
5. Entrapment of large whales in fishing gear in eastern Canada.
6. Incidental kill of harbor porpoise, pilot whales, and gray whales in gillnets in California.
7. Incidental kill of Dall's porpoise in Japanese salmon gillnet fisheries in the North Pacific.
8. Incidental kill of cetaceans in squid and tuna gillnet fisheries of Japan, Taiwan, and Republic of Korea in the central North Pacific.
9. Population trends in dolphins killed incidentally in tuna purse-seine fisheries of the U.S., Mexico, and other nations in the eastern tropical Pacific.
10. Conservation of gray whale breeding habitat in Mexico.
11. Exploitation of harbor porpoise in Greenland.
12. Status of the bowhead population exploited by native peoples in Alaska and Greenland.
13. Status of the bowhead whale in eastern Canada and Greenland.
14. Population identity of humpback whales in the North Pacific and North Atlantic.
15. Status of right whales in the western North Atlantic.

Dolphins killed in gillnets off Sri Lanka are marketed locally for human consumption. (Photograph by A. Alling, courtesy of World Wide Fund for Nature)

South America

16. Protection of spinner dolphin habitat at Fernando de Noronha Island off Brazil.

17. Status of the right whale in the western South Atlantic.

Europe

18. Status of the northern bottlenose whale.

19. Incidental kill of harbor porpoise in gillnets in the eastern North Atlantic.

20. Exploitation of pilot whales at the Faroe Islands.

21. Status of the harbor porpoise in the North Sea and Baltic Sea.

22. Status of the dolphin and porpoise fishery and the exploited populations in the Black Sea.

23. Pollutant levels in dolphin populations of the western Mediterranean.

Africa

24. Recovery of right whales in the eastern South Atlantic.

25. Recovery of right whales off East Africa and stock identity in the Indian Ocean.

26. Incidental kill of small cetaceans in tuna purse-seine fisheries in the eastern tropical Atlantic.

Asia

27. Status of dolphins and small whales exploited in drive and harpoon fisheries in Japan, including dolphin culls.

28. Status of Baird's beaked whales off Japan.

29. Incidental kill of small cetaceans in Japanese coastal fisheries.

30. Status of the finless porpoise in the Sea of Japan.

31. Conservation of river dolphin (*Orcaella brevirostris*) habitat in Indonesia.

32. Monitoring of Indus river dolphin population in Sind, Pakistan.

33. Construction of baiji reserve at Tongling, China.

Australasia

34. Incidental kill of dolphins in gillnet fisheries off Australia.

Worldwide

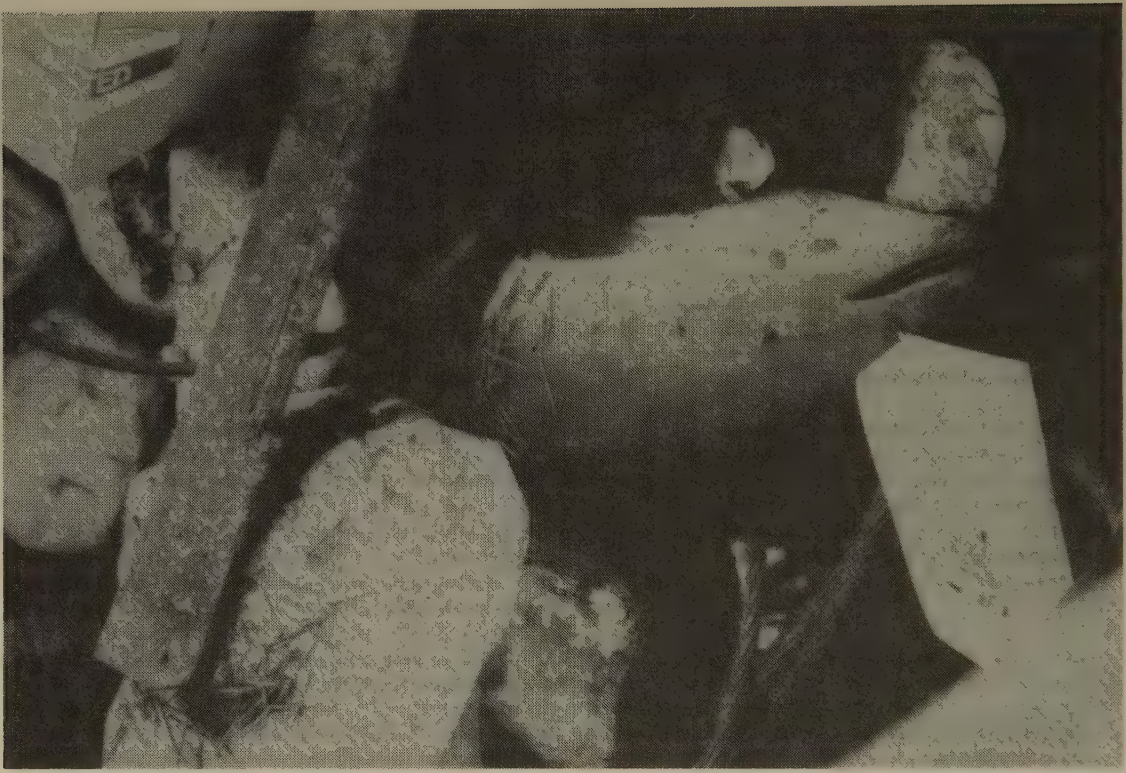
35. Whaling by IWC members under scientific permit.

36. Reporting of by-catches of small cetaceans by IWC members and their dependencies.

37. Local subsistence fisheries (e.g., Solomon Islands, Lesser Antilles, St Helena, Indonesia, Indian offshore islands, Senegal).

38. Interactions between recovering populations of protected whale species and fisheries, including direct conflicts and competition.

39. Effects of pollution on cetaceans.



Harbor porpoise *(Phocoena phocoena)* killed in herring gillnets and other fishing gear in the eastern North Atlantic are usually discarded rather than utilized. (Photo by J. M. Coe)

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Appendix 2

List of National Agencies, Research Institutions, and Conservation Organizations in Problem Areas[1]

North America

1. Centro de Investigaciones Pesqueras
Km 1, Carretera A, Pichilingue
La Paz, B.C.S., Mexico

2. Departamento de Biología Marina
Universidad Autónoma de Baja California Sur
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3. Departmento de Biología, Facultad de Ciencias
Universidad Nacional Autónoma de Mexico
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4. Laboratorio de Mastozoología
Instituto de Biología-UNAM
Apartado Postal 70-153
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5. Centro de Investigaciones Biológicas de Baja California, A. C.
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6. Unidad de Ciencias Marinas
Universidad Autónoma de Baja California
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7. Escuela de Ciencias Marítimas y Alimentarias
Instituto Technológico y de Estudios Superiores de Monterrey—
Unidad Guaymas
Guaymas, Sonora, Mexico

8. Centro Regional de Investigaciones Pesqueras
Instituto Nacional de la Pesca
Guaymas, Sonora, Mexico

South America

1. Sección de Mamíferos
Instituto de Ciencias Naturales
Museo de Historia Natural
Universidad Nacional de Colombia
Apdo. Aéreo 7495
Bogotá, D.E., Colombia

2. División Fauna Terrestre, INDERENA
Apdo. Aéreo 13458
Bogotá, D.D., Colombia

3. Sociedad Colombiana de Ecología
A.A. 24228
Bogotá, D.E., Colombia

4. Centro de Investigaciones
Facultad de Ciencias Exactas y Naturales
Universidad de Antioquía
A.A. 1226
Medellín, Colombia

5. Ministerio del Ambiente y de los Recursos Naturales Renovables (MARNR)
Desarrollo Profesional y Rel. Int.
Apartado 6623
Caracas, Venezuela

6. Fundación para la Defensa de la Natureza (FUDENA)
Apartado 70376
Caracas 1071, Venezuela

7. Sociedad Venezolana de Ciencias Naturales
Apartado 1521, Carmelitas
Caracas 1010-A, Venezuela

8. Sociedad Conservacionista Audubon de Venezuela
Apartado 80450
Caracas, Venezuela

9. Asociación Nacional para la Defensa de la Naturaleza
Qta. Masapo, Ave. Norte
Alta Florida, Caracas 1050, Venezuela

10. Fundación para la Educación Ambiental (EDUCAM)
1ra Avenida, No. 203-102
Campo Alegre Chacao
Caracas, Venezuela

11. Instituto de Recursos Naturales Renovables
Universidad Simón Bolívar
Departamento Estudios Ambientales
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Caracas, Venezuela

12. Instituto Nacional de Pesquisas da Amazônia (INPA)
Departamento de Biologia de Mamíferos Aquáticos
Caixa Postal 478, Cep: 69.000 Manaus
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13. Instituto de Biologia, Sector de Ecologia
Universidade Estadual do Rio de Janeiro
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14. Laboratório de Mamíferos Marinhos
Departamento de Oceanografia
Fundação Universidade do Rio Grande (FURG)
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Rua Miranda Valverde 103, Cep: 22.281
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16. Divisão de Zoologia do Departamento de Biologia
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Cep: 88.000 Campo Grande-MS
Brazil

17. Instituto de Pesquisas da Marinha
Arraial do Cabo
Cep: 28.910 Rio de Janeiro
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18. Instituto Oceanográfico
Universidade de São Paulo
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19. Companhia Energetica de São Paulo (CESP)
Coordenadoro de Meio Ambiente e Recursos Naturais
Av. Paulista, 2064-8o andar
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Parque de Agua Branca
C.P. 1322
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21. Fundação Zoobotanica do Rio Grande do Sul
C.P. 1188
90.000 Porto Alegre-RS, Brazil

22. Instituto Brasileiro de Desenvolvimento Florestal (IBDF)
Departamento de Parques Nacionais e Reservas Equivalentes
Palacio do Desenvolvimento
SBN 13o Andar
70.000 Brasília-DF, Brazil

23. Secretária Especial do Meio Ambiente (SEMA)
Ministério do Interior
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24. Associação Brasileira de Ecologia
Av. Atlantica, 734, Apto. 1201
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25. Associação de Defensa do Meio Ambiente
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26. Fundação Pro-Natureza (FUNATURA)
SHIS-QI 07-CL Bloco B, Sala 201
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27. Departamento do Meio Ambiente
Estado do Rio Grande do Sul
Biblioteca, Av. Ipiranga, 389
90.000 Porto Alegre-RS, Brazil

28. Museo Nacional de História Natural de Montevideo
C. Correo 399
Montevideo, Uruguay

29. Departamento Científico y Tecnólogico
Industria Lobera y Pesquera del Estado
Rbla. Baltasar Brum s/n esq. Fco. Tajes
Montevideo, Uruguay

30. Fundación Vida Silvestre Argentina--Grupo Cetáceos
Leandro N. Alem 968, Cep: 1001 Buenos Aires
Argentina

31. Centro Austral de Investigaciones Científicas (CADIC)
C. Correo 92
Cep: 9410 Ushuaia, Tierra del Fuego
Argentina

32. Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN)
Av. A. Gallardo 470, C. Correo 220
Cep: 1405 Buenos Aires
Argentina

33. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP)
C. Correo 175
Cep: 7600 Mar del Plata
Argentina

34. Centro Nacional Patagónico--CONICET
28 de Julio 28
9120 Puerto Madryn, Chubut
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35. Movimiento Ecológico Argentino
Callao 741
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36. Amigos de la Tierra
Anchorena 633
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37. Fundación NATURA
Av. 6 de Diciembre 5043 y el Comercio
Casilla 243
Quito, Ecuador

38. Departamento de Actos y Organismos Internacionales
Quito, Ecuador

39. Instituto del Mar del Peru (IMARPE)
Box 3732, Esquina General Valle y Gamarra
Apartado-22, Callao, Peru

40. Fundación Peruana para la Conservación de la Naturaleza (FPCN)
Scipión Llona 181-7, Casilla 5396
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41. Pro Defensa de la Naturaleza (PRODENA)
Av. Nicolás de Piérola 742, of. 703
Edificio Internacional
Lima, Peru

42. Centro de Investigación y Manejo de Mamíferos Marinos (CIMMA)
c/o Instituto de Zoología
Universidad Austral de Chile
C. Correo 567
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Contribution of Early Life Stages to Interannual Variability in Recruitment of Northern Anchovy (*Engraulis mordax*)

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Peterman, R. M., M. J. Bradford, N. C. H. Lo, and R. D. Methot. 1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. 45: 8–16.

We tested Hjort's and Lasker's hypotheses that the abundance of recruits in fishes is determined at an early life stage. Using 13 yr of data on components of population dynamics of the well-studied northern anchovy (*Engraulis mordax*), we reconstructed the abundance of anchovy in each year at three stages: eggs, 4.5-d-old yolk-sac larvae, and 19-d-old larvae. No abundance measure was significantly correlated with age 1 recruits, resulting in rejection of Hjort's and Lasker's hypotheses. We give reasons why the low correlations are not an artifact of estimation error. The lack of correlation exists because of the large variability (CV = 171%) in survival rate between age 19 d and age 1 yr. Therefore, attempts to understand interannual variability in recruitment in this, and perhaps other, marine fish species may have to rely not only on data on eggs and larvae, but especially on data on abundances estimated after 20 d, closer to the age at recruitment.

Les hypothèses de Hjort et de Lasker, selon lesquelles le nombre de recrues chez les poissons est déterminé au cours des premiers stades de vie, ont été testées. À partir des données couvrant une période de 13 ans provenant des études sur la dynamique des populations de l'anchois du Pacifique (*Engraulis mordax*), on a retracé l'abondance annuelle des anchois à trois stades différents, soit les stades oeuf, alevin vésiculé de 4,5, et alevin de 19. On n'a observé aucune corrélation significative entre les différentes mesures d'abondance et le nombre de recrues d'âge 1, et les hypothèses de Hjort et de Lasker ont donc été rejetées. On explique pourquoi ces faibles corrélations ne résultent pas d'un artefact dû à l'erreur d'estimation. L'absence de corrélation s'explique par la grande variabilité (CV = 171 %) du taux de survie entre les âges 19 j et 1 a. Pour comprendre la variabilité interannuelle du recrutement chez l'anchois, et peut-être chez d'autres espèces de poissons marins, les données concernant les oeufs et les alevins peuvent être insuffisantes; peut-être serait-il préférable de se fier surtout aux données sur l'abondance après l'âge de 20 j, c'est-à-dire à un âge plus rapproché du moment du recrutement.

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One of the best examples of a paradigm in fish population biology is Hjort's (1913, 1926) hypothesis that the annual abundance of recruits (year-class strength) is established at an early life stage, soon after larvae absorb their yolk sac. This hypothesis was based on the observed high mortality rates of these young fish, and on their planktonic nature, which potentially makes them extremely vulnerable to starvation, predation, and transport by movement of water away from habitats favorable to subsequent growth and survival. This "critical period" hypothesis has stimulated considerable research and has formed the foundation of many attempts to explain interannual variability in recruitment (e.g. Bannister et al. 1974; Cushing 1975; Sinclair et al. 1985). May (1974) and W. C. Leggett (pers. comm.) reviewed the literature and showed that there is not strong support for Hjort's hypothesis, yet it still is the basis of considerable research (e.g. Walsh et al. 1981; Wroblewski 1984; and others).

Lasker's (1975, 1981) stable ocean hypothesis is a special case of Hjort's paradigm. Lasker proposed that wind-driven turbulent mixing of the upper ocean could cause high mortality of first-feeding fish larvae through dissipation and dilution of patches of larval food. Consistent with this is the observation that starvation is the major source of mortality for first-feeding larvae (Theilacker 1986), although this does not appear to be a direct cause of death for older larvae (O'Connell 1980). The second part of Lasker's hypothesis was that these turbulent mixing conditions would lead to a poor year-class.

Recently, Peterman and Bradford (1987) tested the turbulent mixing mechanism of Lasker's stable ocean hypothesis and found that, indeed, high mortality rates of young northern anchovy (*Engraulis mordax*) larvae (up to age 19 d) occurred in years when spawning seasons had many periods of high-speed winds. Years with few periods of high winds were associated with low larval mortality rates. If Hjort and Lasker are correct in hypothesizing that mortality at this early stage has a strong influence on subsequent recruitment, then we should expect a positive correlation between the number of larvae surviving through this early larval period and subsequent recruitment. We arbitrarily defined recruitment as the abundance of fish of age 1 yr.

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For the northern anchovy, previous analyses (Ahlstrom 1965; Methot 1983; Smith 1981) suggest that the number of surviving larvae is *not* related to recruitment. However, no correlation statistic was calculated in these cases either because of too few years of data (Methot 1983) or because only qualitative indices of recruitment were available. Both limitations have been rectified; estimates of age 1 recruitment since 1965 are now available from stochastic virtual population analysis (VPA) (Methot 1986, 1988).

In this paper, we reconstruct the annual abundance of northern anchovy at each of several early life stages, using in most cases annual observations on components of egg production and on mortality rates of eggs and larvae. We then estimate the extent to which interannual variation in abundance at each of these early life stages contributed to interannual variation in abundance of age 1 recruits of northern anchovy from 1965 to 1985. Thus, we test Hjort's and Lasker's hyotheses for this northern anchovy population.

Methods

We used data on the central population of northern anchovy, which spawns primarily during January–April in waters off the coast of southern California. This species is one of the dominant fish in the California Current, with a mean spawning biomass of 500 × 10^3 metric tonnes (t) from 1965 to 1985 (Methot 1986), and it has been intensively studied since the 1950's by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) (see annual volumes of CalCOFI Reports and Smith 1985).

To initiate the reconstruction of abundances of early life stages (eggs, yolk-sac larvae, and 19-d-old larvae or prerecruits), we used numbers of fish at each age from 1 to 5+ yr estimated for 1965–85 by Methot's (1986) VPA (Table 1).

Egg Production, E

Total egg production by the anchovy population in a given year, E_j, was estimated by

$$(1)\quad E_j = \sum_{i=1}^{5} 0.5 N_{ij}\, p_{ij}\, F_{ij}\, S_{ij}\ ,$$

where i = age-class, j = year, 0.5 = fraction of females (Bindman 1986), N_{ij} = number of adults by age and year, from Table 1, p_{ij} = proportion of fish mature in each age by year, F_{ij} = batch fecundity (eggs per female per spawning), and S_{ij} = spawning frequency, or number of spawnings per year per female of age i.

A constant sex ratio was used because annual estimates are unreliable due to small samples and a tendency for segregation between sexes in survey catches (Klingbeil 1978).

TABLE 1. Millions of fish at time of spawning in each age group of the central population of northern anchovy. Data from Methot's (1986) virtual population analysis. This table only shows data for those years that were relevant to the analysis (other years had no data on early life stages).

Year	Age 1	Age 2	Age 3	Age 4	Age 5+
1965	10 794	5 744	1 965	1339	635
1966	5 494	5 695	2 917	959	924
1969	14 241	7 779	1 707	473	528
1972	56 233	26 496	5 151	1013	375
1975	17 806	21 822	17 177	6118	2547
1978	9 390	13 462	1 211	754	1099
1979	76 561	3 457	4 276	355	500
1980	58 144	24 737	885	966	170
1981	45 273	18 913	6 634	208	233
1982	15 537	11 063	3 319	908	47
1983	51 305	3 667	1 728	392	84
1984	24 174	17 641	1 046	438	107
1985	54 693	8 980	5 718	313	150

The proportion of females of a given age which was mature was set = 1.0 for ages ≥2 based on Parrish et al. (1986) and, for age 1 fish only, was made an increasing function of the mean January–February water temperature as measured at Scripps pier (Methot 1986). For years when the fraction of mature age 1 fish was estimated from field samples (Methot 1986), we used the mean of this estimate and the one predicted for that year from the water temperature by Methot's (1986) temperature-dependent function (Table 2). This approach reflects the imprecision of the field samples. In years without field samples, we used Methot's function and the observed temperature to estimate age 1 maturity.

Because northern anchovy are multiple spawners with an indeterminate annual fecundity (Hunter and Macewicz 1980), we estimated the number of eggs produced per mature female per year from two components: eggs per female per spawning (batch fecundity) and number of spawnings per year per female (spawning frequency).

Batch fecundity, F

Eggs per female per spawning (F) was calculated from the batch fecundity relations reported by Hunter et al. (1985), which are linear functions of female weight:

$$(2)\quad F_{ij} = a + b(0.95W_{ij}).$$

The weight of each female of age i in year j was multiplied by 0.95 because Hunter et al.'s (1985) batch fecundity relations used gonad-free weight which is 95% of total weight (Hunter and Macewicz 1980). Table 2 gives the annual values for the a and b parameters in equation (2); long-term mean parameter values (Hunter et al. 1985) were used in years when field estimates of batch fecundity relations were not available. Annual weights of female spawners at each age (Table 3) were obtained from California Department of Fish and Game surveys (Methot 1986). Again, long-term means were used for years when it was not possible to estimate weights from field samples.

Spawning frequency, S

Parrish et al. (1986) showed that older females produce more egg batches per year than small females. We therefore used the following relation between number of egg batches per female per year (spawning frequency, S) and weight:

$$(3)\quad S_{ij} = c + dW_{ij},$$

where $c = -6.136$, $d = 1.2878$, and W_{ij} = weight (grams). Paramaters c and d were estimated by linear regression of our "adjusted" version of Parrish et al.'s (1986) data for number

TABLE 2. Annual parameter estimates for components of egg production and mortality of eggs and larvae by the year in which spawning occurred. Maturity, p_1, is the fraction of age 1 females which were mature in year j. Fecundity parameters a and b refer to equation (2); missing parameter estimates were filled in with long-term means, denoted by an asterisk. Embryo mortality parameters α and t refer to equation (4) and larval mortality parameters β and u to equation (5). Age 1 recruits are those resulting from spawning in the year given in column 1. Data sources are given in the text.

Year (j)	Maturity (p_1)	Fecundity		Embryo mortality		Larval mortality		Age 1 recruits (10^6)
		a	b	α	t	β	u	
1965	0.28	−1104*	583*	0.19	4.91	2.42	18.27	5 494
1966	0.57	−1104*	583*	0.42	4.91	1.84	20.35	7 911
1969	0.82	−1104*	583*	0.19	4.79	2.15	18.33	23 675
1972	0.10	−1104*	583*	0.25	4.54	1.73	18.35	68 509
1975	0.23	−1104*	583*	0.44	4.89	1.88	18.95	10 617
1978	0.99	−1104*	583*	0.59	4.24	1.66	19.47	76 561
1979	0.55	−4410	658	0.48	4.91	2.22	18.62	58 144
1980	0.98	−1891	535	0.36	3.05	1.22	18.63	45 273
1981	0.92	−1979	714	0.38	3.10	1.53	18.56	15 537
1982	0.75	−180	586	0.36	4.42	1.81	18.13	51 305
1983	0.96	−1002	559	0.46	3.82	2.05	18.88	24 174
1984	0.94	−554	505	0.36	4.26	1.47	19.74	54 693
1985	0.63	−2040	648	0.28	4.93	2.13	20.96	47 011

TABLE 3. Total weight (g) per spawning fish. Data from Methot (1986), derived from California Department of Fish and Game winter surveys. Years with missing data (denoted by an asterisk) were filled in with the long-term mean for that age.

Year	Age				
	1	2	3	4	5+
1965*	8.7	14.6	18.3	21.2	24.3
1966*	8.7	14.6	18.3	21.2	24.3
1969*	8.7	14.6	18.3	21.2	24.3
1972*	8.7	14.6	18.3	21.2	24.3
1975*	8.7	14.6	18.3	21.2	24.3
1978	10.4	15.4	19.7	22.2	22.2
1979	9.2	18.3	21.7	24.8	24.3
1980	7.1	15.0	17.9	24.8	29.5
1981	9.8	13.4	18.3	20.2	27.7
1982	9.5	16.6	18.8	21.2	22.2
1983	8.9	11.0	17.5	19.7	24.3
1984	4.8	12.4	13.8	18.8	22.2
1985	10.6	15.4	18.4	21.2	24.3

of egg batches for fish aged 1, 2, and 3 yr on our mean spawning weight at those ages (r = 0.996).

We "adjusted" Parrish et al.'s (1986) data as follows. These authors provided age-specific monthly spawning frequencies (number of egg batches per female per year) for each age 1–3 and age 4+ fish, averaged over many years. However, for age 1 fish, the spawning frequencies in Parrish et al. (1986) were calculated from samples which included immature fish. To obtain an estimate of spawning frequency of *mature* age 1 fish only, we divided Parrish et al.'s (1986) spawning frequency for all age 1 fish by the average fraction of age 1 fish that matured during those years. This fraction was 0.905, as estimated by the fraction of age 1 fish mature during March, the month with the highest mean proportion of spawning age 1 fish (Parrish et al. 1986). This method assumed that the fish that were immature in that month would not spawn at all that year. In addition, the monthly spawning frequencies for all ages were divided by 0.95, a correction for sampling bias noted by Parrish et al. (1986). The resulting "adjusted" estimates of spawning frequency were used to estimate the parameters of equation (3) by regression.

The number of spawnings each year for mature age 1–3 fish was the sum of the monthly spawning frequencies for each age over the 12-mo interval, December–November. November was the month with least spawning and formed a natural break in the annual spawning cycle.

We then estimated the spawning frequencies for each age in each year from equation (3), using weights of spawning females of each age in that year. The product of the components shown in equation (1) thus gave an estimate of the total number of eggs produced each year by the central population of northern anchovy.

Early Larvae, L

Lo (1985) calculated the mean instantaneous daily mortality rate of each annual cohort of eggs between time of spawning and mean age of yolk-sac larvae. We used her "Series 2" estimates of this rate, α (see Table 2). Lo also estimated the time between these two stages, t, for each year (Table 2) because it was affected by water temperature (Lo 1983). The mean age of yolk-sac larvae from data in Table 2 averaged 4.4 d from time of spawning; such larvae were 3–4 mm in length (Lo 1983). Standard CalCOFI sampling cruises for eggs and larvae were made only every third year between 1966 and 1978; thus, our analysis here is limited to the 13 yrs sampled by CalCOFI between 1965 and 1985, when both age 1 recruitment data and egg mortality data were available (see section on Recruits below). We used Lo's (1985) equation to calculate the number of eggs surviving to mean age of yolk-sac larvae (L_j):

$$(4) \quad L_j = E_j e^{-\alpha_j t_j}$$

where α_j = instantaneous daily mortality rate in year j and t_j = temperature-dependent mean age of yolk-sac larvae in year j, in days since fertilization. Annual values for the α_j and t_j parameters are given in Table 2. In this species, first feeding of larvae is initiated only after the yolk is absorbed (Theilacker and Dorsey 1980). Thus, abundance of the yolk-sac larvae, L_j from equation (4), is estimated just prior to onset of first feeding.

Prerecruit Larvae, PR

Lo (1985) also estimated for each year the mortality coefficient of larvae from the mean age of yolk-sac larvae (just before the start of first feeding) to an average of 19 d after spawning (~10 mm length). Larvae larger than this were not included in the analysis because of their increased ability to avoid standard bongo nets (Smith 1981; Hewitt and Methot 1982: Folkvord and Hunter 1986; Lo 1986). This early larval period spans yolk-sac absorption, initiation of first feeding, and the early larval stage up to 19 d of age. To simplify terminology, we refer to the latter, 19-d-old larvae as prerecruits. Lo (1985) assumed that mortality rate varied with larval age, and she estimated the duration of this period for each year. Table 2 gives her annual estimates of the β mortality coefficient and times at the beginning and ending of this period, *t* and *u*, respectively. We then calculated for each year the survival of yolk-sac larvae, L_j, to prerecruits, PR_j, with Lo's (1985) equation:

(5) $PR_j = L_j (u_j/t_j)^{-\beta_j}$

where t_j = same as in equation (4) and u_j = mean age of larvae at end of the sampled period in year *j*, in days since fertilization.

Recruits, *R*

Because no field estimates exist for annual mortality rates between prerecruits (19-d-old larvae) and age 1, we obtained annual estimates of abundance of age 1 recruits, R_j, from Methot's (1986) virtual population analysis. These recruits (Table 2) represent abundance as of 15 February each year. Thus, the 1966 estimate of 5494 × 10^6 age 1 fish is the recruitment at age 1 resulting from spawning in early 1965. Because no reliable adult age structure data were available before 1965, our data set for age 1 recruits was restricted to 1965 and later. This excluded the pre-1965 data on earlier life stages from our analysis of the effect of these early stages on subsequent recruitment.

Life Table

To compare the extent of mortality suffered by a cohort during each life stage up to recruitment, we calculated standard survival rates (*s*, not to be confused with *S*, which is spawning frequency as defined above) and instantaneous mortality rates for each year:

(6) $s_{j1} = L_j/E_j,$
$s_{j2} = PR_j/L_j$
$s_{j3} = R_j/PR_j$

where the second subscript, k = 1, 2, or 3, on *s* indicates the life phase. These fractions surviving were also converted to total instantaneous mortality rates for the respective periods:

(7) $M_{jk} = -\log_e (s_{jk})$.

We used statistics on these 13 yearly M_{jk} to construct a life table for the central population of northern anchovy.

Analysis

We took natural logarithms of abundances at all stages to calculate correlations because recruitment of marine fishes is frequently lognormally distributed (Hennemuth et al. 1980) and because logarithms of our abundances did not deviate substantially from a normal distribution (although there were too few data points to test this formally).

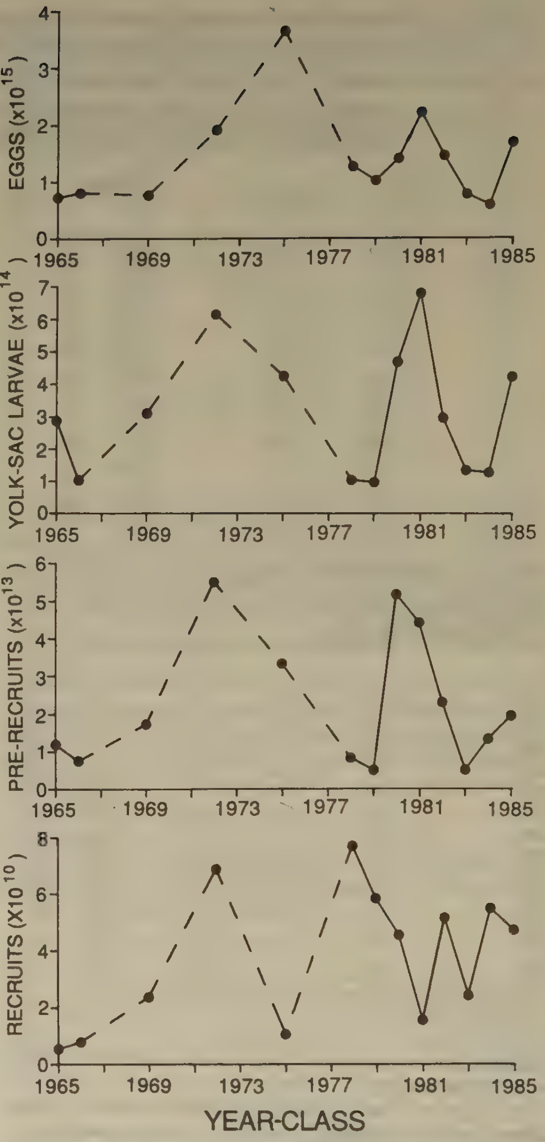

FIG. 1. Estimated abundances of early life stages for the central population of northern anchovy by year-class. Abundances of the first three stages are from this paper, and age 1 abundances are from Methot's (1986) VPA. Broken lines connect CalCOFI survey years before 1978, in which early life history variables were estimated only every third year from 1966 to 1978. Actual abundances in non-CalCOFI years could have been much higher or lower than the locations of the broken lines; dashes are provided only to aid comparison of observed points.

Results and Discussion

Recruitment Variability

Figure 1 shows estimated annual abundances of each life stage for the northern anchovy and Table 4 gives summary

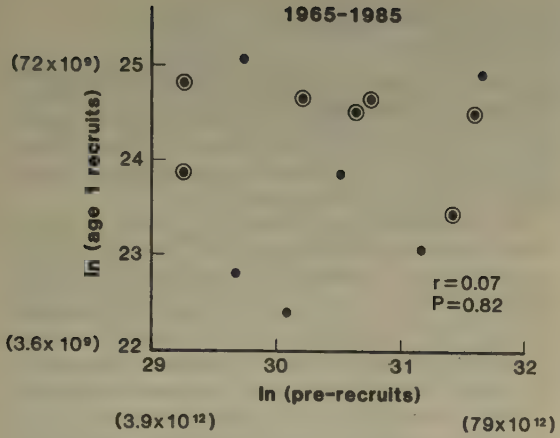

FIG. 2. Relationship between $\log_e$(prerecruit abundance, ~age 19 d) and resulting abundance of $\log_e$(age 1 recruits) for 1965–85 year-classes. Circled data points are from those years in which all components in the reconstruction of prerecruits were observed (see General Discussion section).

TABLE 4. Summary statistics of the 13 yr of abundances of northern anchovy, in numbers at each stage. Geometric mean column is the mean of the natural logs of abundances.

Stage	Arithmetic mean	Standard deviation	CV	Geometric mean
Eggs	1.40×10^{15}	8.39×10^{14}	0.599	34.74
Larvae (4.5 d)	3.12×10^{14}	1.99×10^{14}	0.638	33.16
Prerecruits (19 d)	2.26×10^{13}	1.76×10^{13}	0.780	30.44
Recruits (1 yr)	3.76×10^{10}	2.42×10^{10}	0.643	24.07

TABLE 5. Correlations, r, between reconstructed abundances at early life stages and subsequent age 1 recruitment from that same cohort for the central population of northern anchovy. In each correlation, the $\log_e$ was taken of both abundance variables. P is the probability for the null hypothesis H_0: $r = 0$, and sample size = 13 yr in all cases. Average age since spawning is given in parentheses.

Beginning stage	Ending stage	r	P
Eggs	Age 1	0.04	0.89
Yolk-sac larvae (4.5 d old)	Age 1	−0.09	0.76
Prerecruits (19-d-old larvae)	Age 1	0.07	0.82

TABLE 6. Correlations, r, between reconstructed abundances at life stages prior to recruitment for the central population of northern anchovy. $\log_e$ of both abundances were used in each correlation, and sample size = 13 yr in all cases.

Beginning stage	Ending stage	r	P
	Across one stage		
Eggs	Yolk-sac larvae (4.5 d old)	0.66	<0.015
Yolk-sac larvae (4.5 d old)	Prerecruits (19-d-old larvae)	0.91	<0.001
	Across more than one stage		
Eggs	Prerecruits (19-d-old larvae)	0.67	<0.014

TABLE 7. Statistics on instantaneous mortality rates (M) of northern anchovy, calculated from 13 yr of reconstructed abundances at successive life stages. SD_M is the standard deviation of M. The mean daily M was calculated as the mean total M from the beginning to the end of the period, divided by the duration of the period (in days).

Beginning of period	End of period	Mean duration of period (d)	Mean total M over period	SD_M	Mean daily M
Eggs	Yolk-sac larvae	4.4	1.584	0.544	0.360
Yolk-sac larvae	Prerecruits	14.6	2.711	0.343	0.186
Prerecruits	Age 1 recruits	346	6.378	1.170	0.018

statistics.

Analysis of our 13 yearly abundances of early life stages and age 1 recruitment does not support Hjort's or Lasker's hypothesis that recruitment is established at an early stage in northern anchovy. No correlation between abundance at early life stages and recruitment was significant, including the one between age 1 recruits and prerecruits (those larvae which survived through 19 d) (Fig. 2; Table 5). Thus, even though the wind speed index of turbulent mixing explained 65% of the interannual variation in larval mortality during the "critical" first-feeding phase (Peterman and Bradford 1987), the numbers of larvae surviving through this period were not correlated with subsequent recruitment (r was only 0.07). Hjort's and Lasker's hypotheses thus are not applicable to our 13 yr of data.

Mortality between the larval stage at 19 d old and age 1 is sufficiently variable among years to destroy the correlations between abundance at all early life stages and recruitment. However, variable mortality *prior to* 19 d is not the cause of these low correlations. Lo's (1985) estimates of mortality rates and time at stage varied among years but still led to significant correlations between egg abundance and resulting yolk-sac larvae and between these larvae and subsequent prerecruits (Table 6). Yet neither the correlation between eggs and age 1 recruits nor the correlation between yolk-sac larvae and age 1 was significant (Table 5). Based on instantaneous mortality rates (Table 7), mean survival through the stage from prerecruits to age 1 was lowest of the three stages (Table 8); only 0.34% of the 19-d-old larvae survived to age 1 recruits, on average. Most important, however, this stage was the most variable, having a coefficient of variation (CV) in survival rate of 1.71, almost three times that of the egg-to-larval stage (Table 8). Thus, the interannual variability in mortality between successive early life stages (egg-to-larvae, larvae-to-prerecruits) was not sufficient to destroy a significant correlation between abundances at those stages, but the large variability in the fraction of fish surviving from prerecruits to recruits did destroy any correlation between abundance at earlier life stages and age 1 recruitment. Therefore, recruitment strength is not determined at the early life stages.

As originally stated, Hjort's and Lasker's hypotheses about sources of interannual variation in recruitment referred specifically to the importance of the early larval stage, within a few days of yolk-sac absorption. However, for the anchovy population analyzed here, the early larval stage averages only 14.5 d in duration, which is only a small portion of the total duration as larvae (about 20%; Hunter and Coyne 1982) and a smaller portion of the egg-to-recruitment period. Based on the highly variable mortality after age 19 d reported here, it appears that the "critical period" (if one exists) is more likely to occur at a later stage than the early one discussed by Hjort and Lasker.

Our low correlation between 19-d-old larvae and age 1 abundance does not imply that the lack of correlation will also hold when abundance of prerecruits gets very low and outside the range of our data. Extremely low abundance of prerecruits could lead to significantly decreased recruitment, but our data do not permit a test of this hypothesis.

Regardless of the reason for lack of correlation between abundances of prerecruits and recruits, current data clearly show that it is not possible to forecast age 1 abundance from larval abundance at 19 d or before. If forecasts are needed, they will have to be made from population measures taken at an age between 19 and 365 d. Indeed, Methot (1986) showed that a reasonable index of age 1 recruits is the proportion of age 0 (not yet 1 yr old) fish caught by the Mexican commercial fishery during their 9th through 12th mo of life, just prior to becoming age 1 fish. The proportion of these age 0 fish reflects the size of the incoming year-class: the arcsine or angular transform (Sokal and Rohlf 1969, p. 386) of the proportion of these age 0 fish is significantly correlated with the $\log_e$ of age 1 fish ($r = 0.75$, $r^2 = 0.57$, $P < 0.01$). An identical analysis of the proportion of age 0 fish in their *third* quarter of life (6–9 mo old) shows much lower correlation with age 1 fish ($r = 0.33$, $r^2 = 0.11$, $P > 0.4$), as does the relation between this third quarter index and our $\log_e$(prerecruit abundance) ($r = -0.07$). The fourth quarter correlations particularly confirm that better forecasts of recruitment will arise from samples at ages closer to age 1 than the early larval stage.

Life Table

Mean instantaneous *daily* mortality rates for the three periods described here decrease with increasing age and size of northern anchovy up to age 1 (last column of Table 7), as has been found for numerous other species (e.g. Cushing 1974; Dahlberg 1979; Peterson and Wroblewski 1984). The means of the reconstructed abundances on which the M values in Table 7 are based appear reasonable because the mean instantaneous mortality rate for each period (plus symbol in Fig. 3) agrees well with theoretical expectations and with rates observed for other fishes at a similar size (Fig. 3). Note that the mean instantaneous daily mortality rate of 0.018 for the period between prerecruits and age 1 applies over a longer time (averaging 346 d) than the larger daily mortality rates at previous stages. The net result is a large mean total instantaneous mortality over the period from prerecruits to recruits (~6.4, Table 7).

The mean daily instantaneous mortality rates for the first two periods in Table 7 are slightly different from those in Smith's (1985) summary life table: 0.25 and 0.16 instead of the 0.36 and 0.186 estimated here. This is partly because Smith's estimates were from a subset of the 13 yr used here. Our value of 0.018 for the daily mortality rate from prerecruits to age 1 recruits falls within Smith's range for that period (0.01–0.05).

General Discussion

Estimation Error

Some readers may believe that the low correlation between abundances of prerecruits and recruits (Fig. 2) is due to errors in estimation of the components of the reconstruction process, rather than due to biological reality. There are a number of lines of evidence which suggest that estimation errors are *not* the explanation for this low of correlation.

First, the correlation was still low ($r = -0.21$, $P = 0.64$) when we only included data from those years in which all components were observed, rather than estimated by filling in the long-term mean. The points included (circled dots in Fig. 2) thus had less error embedded in them than the points in the original analysis. Note that these seven relatively error-free points covered the same range in abundance of prerecruits as the original 13 (Fig. 2), yet no significant correlation emerged.

Second, imprecision in the mortality estimates prior to 19 d was probably not the cause of the low correlation between our reconstructed abundance at that age and age 1 recruits. Lo's (1985) annual mortality coefficients for the periods between eggs and 19-d-old larvae were based on a large number of ichthyoplankton tows (~1000) (Lo 1986). Also, the high correlations in Table 6 among eggs, yolk-sac larvae, and prerecruits were all statistically significant and show that variation in mortality rates due to natural and sampling variability at those early stages contributes little to the low correlations between those early stages and recruitment (all of the latter r values were near zero, Table 5).

In addition, one must assume an unreasonably large amount of estimation error in the abundance of prerecruits to show that the correlation of 0.07 found here between prerecruits and recruits was derived from a stronger true underlying correlation. Under the assumption that the $\log_e$(prerecruits) are normally distributed, we used methods described by Snedecor and Cochran (1967, p. 165) to reestimate the correlation coefficient with estimation error removed from the prerecruit abundance. With parameters estimated from the correlation of $\log_e$(recruits) on $\log_e$(prerecruits), extremely large estimation errors are required to strengthen the correlation. For example, if estimation error accounts for 50% of the total variation in $\log_e$(prerecruits), the correlation coefficient only increases from 0.07 to 0.10; if it accounts for 80% of the variance in X, r is only increased to 0.16. Therefore, we conclude that estimation error alone is not sufficient to give rise to the low correlation that we observed.

Finally, the estimates of age 1 abundance appear precise. The time series of abundance of recruits which was used here was from one VPA based on one set of assumptions used by Methot (1986). However, two other time series of recruits were derived using other assumptions, and all three are significantly correlated (all $r > 0.83$, Methot 1986). In part, this consistency among the different time series of recruits arose because Methot (1986) used in his VPA four independent data sets on age compositions, which were in turn highly correlated (r values ranged from 0.61 to 0.99). Thus, it is unlikely that imprecise estimates of age 1 abundance are the cause of the lack of correlation between prerecruits and age 1 recruits.

Given these reasons, estimation error does not appear to be an important factor in our results. The lack of correlation between prerecruits and age 1 recruits in northern anchovy appears real and it is caused by the highly variable survival rate during that lengthy period.

TABLE 8. Statistics on proportion of northern anchovy cohorts surviving. Following standard formulae for lognormal distributions (Aitchison and Brown 1966), we calculated these statistics for survival rates (proportions) from the mean, μ, and variance, σ^2, of the corresponding instantaneous mortality rate (M) data shown in Table 7. Median of the 13 yr of survival rates was $e^{-\mu}$, their mean was $e^{(-\mu+(\sigma^2/2))}$, and their coefficient of variation (CV) was $(e^{\sigma^2} - 1)^{0.5}$. Last column shows mean fraction of initial eggs which survived through to the end of the period indicated.

Beginning of period	End of period	Mean duration of period (d)	Median survival rate over period	Mean survival rate over period	CV	Mean daily survival rate	Mean fraction of eggs
Eggs	Yolk-sac larvae	4.4	0.205	0.238	0.587	0.722	0.238
Yolk-sac larvae	Prerecruits	14.6	0.066	0.070	0.353	0.833	1.67×10^{-2}
Prerecruits	Age 1 recruits	346	1.7×10^{-3}	3.4×10^{-3}	1.712	0.984	5.66×10^{-5}

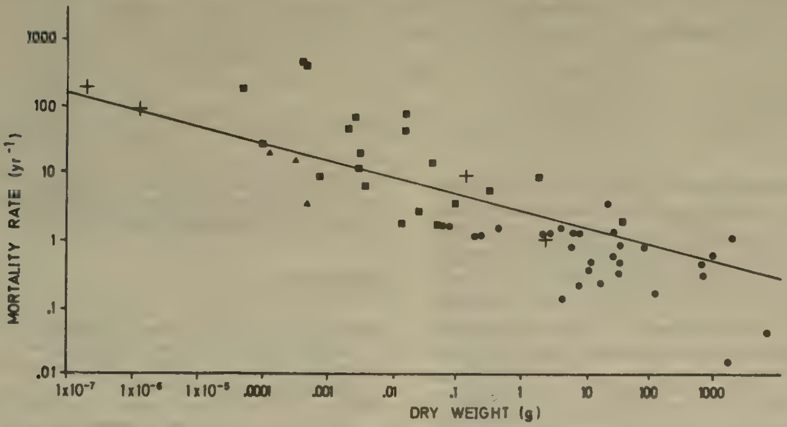

FIG. 3. Instantaneous mortality rates of different species of fish and chaetognaths in relation to body weight. Plus symbols are for the three early life stages of northern anchovy discussed here, plus anchovy adults. All data except northern anchovy are from Peterson and Wroblewski (1984). Mean body weight of northern anchovy during each of the three early life history periods in the life table was the weighted average (weighted by abundance) calculated from a survivorship curve derived from our estimated instantaneous daily mortality rate for that period (shown in Table 7) and a growth curve. We used Hunter's (1976) growth curve of dry weight vs. age for eggs to 19-d-old larvae, and from then until age 1, we used Methot's (1981) observed lengths at age converted to dry weight by his length–weight relationship.

We concur with May (1974) and W. C. Leggett (pers. comm.) that there is evidence to doubt the generality of Hjort's hypothesis that mortality of first-feeding larvae is a strong determinant of year-class strength. If we are to improve our understanding of causes of variability in recruitment of northern anchovy, research must be done on all life stages, especially those closer to age 1. Methot's (1986) correlations between recruits and proportion of age 0 fish in the Mexican catch underscore the importance of understanding the sources of variability in mortality even during the last 3 mo prior to recruitment as age 1 fish. Although the majority (57%) of interannual variability in age 1 abundance is accounted for by that fourth quarter index, there still is a large amount (43%) of unexplained variability in that period.

Other Species

Much of the research on the early life history of northern anchovy has been directed toward back-estimation of spawning biomass (Lasker 1985). But in addition, the CalCOFI program has been useful from the viewpoint of providing data to rigorously test hypotheses about sources of variability in recruitment of northern anchovy. However, it is not possible to extend our conclusions to other marine fish species with pelagic larvae because they differ from northern anchovy in the physical habitat and the species complexes of predators, competitors, and food organisms. Such differences could lead to differences in the mechanisms that cause variability in recruitment. However, to the extent that fish larvae of similar size face similar problems everywhere, our results suggest that early larval sampling programs alone will provide only a partial understanding of sources of variation in recruitment.

The question concerning the general appropriateness of data on early larval abundances alone can be answered partly by examining the literature that reports analyses of correlations between abundance of recruits and abundance at some earlier life stage. Such correlations are normally used to forecast recruitment for management purposes. Therefore, the summary

Table 9. Summary of reported correlations between abundances at early and later life stages. Sizes of fish, when reported, are given in parentheses below the age. References: A, Cushing (1974); B, Bannister (1978); C, Rauck and Zijlstra (1978); D, Tormosova (1980); E, Postuma and Zijlstra (1974); F, Burd (1985).

Species	Beginning stage	Ending stage	*N* (yr)	Correlation	*P*	Reference
Baltic cod	30-d-old larvae	Age 1 group	6	0.81	0.05	A
	Age 0 group	Age 1 group	6	0.90	0.015	A
North Sea plaice	Eggs	Age 2	10	0.25	0.49	B
	Age 0 group	Age 2	14	0.71	0.005	C
North Sea sole	Age 0 group	Age 2		Low		C
	Age 1 group	Age 2	12	0.68	0.13	C
North Sea haddock	First-feeding larvae (≥6 mm)	Age 2	7	0.60	0.15	D
North Sea herring						
Downs stock	30-d-old larvae	Age 3	15	0.34	0.22	E
	30-d-old larvae	Age 0	13	0.76	<0.01	F
Doggerbank stock	Small larvae (<11 mm)	Age 3	9	0.58	0.10	E
	Large larvae (≥11 mm)	Age 3	9	0.71	0.025	E
Bank stock	20-d larvae	Age 0	11	0.66	0.027	F

of published correlations in Table 9 may be biased towards significant cases because nonsignificant results would be less likely to be reported in the literature. Even so, results in Table 9 are diverse; some stocks show significant correlations and others do not. This diversity of results emphasizes the varied effect of different physical and biological processes on the relative variability in mortality at early and late life stages. Future investigations could fruitfully use a comparative approach (Bakun 1986) to determine which habitat factors are more variable for species such as northern anchovy, which show a low correlation between early larval abundance and recruitment, than for species showing a high correlation.

Table 9 also supports the intuitive reasoning that the closer that abundance samples are taken in time, the more likely a significant correlation is to exist between those abundances. This is demonstrated by Baltic cod (*Gadus morhua*), North Sea plaice (*Pleuronectes platessa*), North Sea haddock, (*Gadus aeglefinus*), North Sea sole (*Solea solea*), Downs herring (*Clupea harengus*), and Doggerbank herring (Table 9). For example, the Downs herring stock in the North Sea showed a lower correlation between abundance of 1-mo-old larvae and an index of recruitment at age 3 (Postuma and Zijlstra 1974) than was observed between those larvae and an index of age 0 fish. Such evidence supports our finding that in the northern anchovy, abundance of age 1 recruits may be better correlated with abundance at some stage closer to age 1 than the currently sampled 19-d-old larvae.

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REVISED ESTIMATES OF HISTORICAL SPAWNING BIOMASS OF THE PACIFIC MACKEREL, *SCOMBER JAPONICUS*

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ABSTRACT

We present revised spawning biomass estimates for the Pacific mackerel stock off southern California for the years 1929–69. These new estimates include corrected assumptions about fecundity, individual growth, underreporting of catches, and the distribution of fishing effort throughout the season. The time series of new estimates shows a more pronounced spawning population decline preceding the population's collapse.

Spawning appears to be more limited to the older fish than previously thought; cumulative egg production curves reveal an increased impact of exploitation on spawn production. Such a pattern might reduce the stock's stability at high levels of exploitation. In examining the weight-at-age time series, we observed clear evidence of density-dependent growth; fish attained much higher weights at age when the population size was small.

RESUMEN

Re-estimaciones de la biomasa de desove de la macarela del Pacífico frente al sur de California son presentadas para el período 1929–69. Estos nuevos valores incluyen suposiciones actualizadas en cuanto a fecundidad, crecimiento individual, declaración de capturas inferiores a las reales, y distribución del esfuerzo pesquero a través de la temporada. La serie de tiempo de las nuevas estimaciones indica una disminución más pronunciada de la población de desove que precedió al colapso de la población.

El desove parece estar más restringido a los peces de mayor edad, con respecto a análisis previos. Las curvas acumulativas de producción de huevos revelan un mayor impacto de la explotación sobre la producción de desove. Un patrón de este tipo puede reducir la estabilidad de la población cuando es expuesta a altos niveles de explotación. La serie de tiempo de peso por edad entrega clara evidencia de crecimiento dependiente de la densidad de la población; los peces alcanzaron mayores pesos a cierta edad cuando el tamaño de la población era chico.

INTRODUCTION

The California stock of *Scomber japonicus*, known locally as Pacific mackerel and elsewhere as chub mackerel, is one of the most closely monitored fish stocks in the world. A remarkably long record of fishery data has made it possible to compute virtual population analyses for the period from the beginning of the fishery in 1929 until the stock's collapse in the late 1960s. After the California legislature closed the fishery in 1970, the stock rebounded, and the fishery reopened in 1977. This provided a second period of catch data. The stock's population dynamics have been described by Parrish and MacCall (1978), MacCall et al. (1985), and Prager and MacCall (1988).

Recent advances in virtual population analysis (Sims 1982; MacCall 1986; Prager and MacCall 1988), new research about the Pacific mackerel's fecundity by Dickerson and Macewicz[1], and a critical reanalysis of the existing growth data (this paper) allowed us to compute corrected historical abundance estimates of the stock's spawning biomass. These estimates differ in several respects from the previous ones.

COMPUTATION OF SPAWNING BIOMASS ESTIMATES

The following formulation was used to compute each year's spawning biomass.

$$B_i = \sum_{j=1}^{5} N_{ij} w_{ij} m_j \qquad (1)$$

where i = an index of year,
j = an index of age,

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[1] Dickerson, T. L., and B. J. Macewicz. MS. Spawning frequency and batch fecundity of chub mackerel, *Scomber japonicus*, during 1985. Available from B. J. Macewicz, Southwest Fisheries Center, P. O. Box 271, La Jolla, CA 92038.

B_i = the spawning stock biomass estimate in year i,
N_{ij} = the number of fish of age j in the population at the beginning of year i,
w_{ij} = the mean weight of a single fish of age j in year i,
m_j = an index of the relative weight-specific egg production (fecundity) of female fish at age j.

Equation 1 relies upon two main assumptions. First, egg production per gram of total weight is assumed constant for the ages in question, except for the effects of m_j. Second, the sex ratio is assumed to remain constant. With these assumptions met, B_i gives relative values of egg biomass spawned from year to year. This quantity is intrinsically relative, both because m_j is a relative index and because no attempt is made to estimate actual egg production per gram of fish weight. Pacific mackerel exhibit indeterminate fecundity (i.e., the total number of eggs to be spawned is not fixed at the beginning of the season, and new oocytes are recruited if feeding and environment are favorable); therefore actual egg production from a given spawning biomass may vary from year to year.

Estimated spawning biomass, then, comprises three elements (numbers, weights, and fecundities at age), which are treated in the following three sections. We report fish weights and biomasses in the English system of measurement because management and monitoring of this fishery have not yet converted to the metric system.

NUMBERS AT AGE

Methods

The estimates of numbers at age were obtained by virtual population analysis (VPA), as in past analyses of this stock's population dynamics (Parrish and MacCall 1978; MacCall et al. 1985). Our first change to past methods was to obtain an estimate of underreporting in the catch statistics. Because no theoretical framework existed for doing this, we relied upon estimates by those involved in management of the fishery (R. Klingbeil, Calif. Dept. of Fish and Game, 245 W. Broadway, Long Beach, CA 90802, pers. comm.). We believe that this approach, while not ideal, is preferable to assuming that no underreporting has taken place (or, almost equivalently, assuming that the degree of underreporting has been constant). Table 1 indicates the degree of underreporting assumed to have taken place, and by which we corrected the catch data before performing VPA.

TABLE 1
Underreporting Percentages Used for Analysis of Pacific Mackerel Catch Data

Years	Underreporting
1929–47	10%
1948–49	9%
1950–51	8%
1952–57	7%
1958–61	6%
1962–69	5%

Our second revision concerned the VPA methodology used to estimate numbers at age from the catch data. VPA methodology has been well described (Murphy 1965; Pope 1972; MacCall 1986), and thus is not reviewed here. However, we made several modifications to the VPA techniques used in prior analyses of this stock. VPA, since it assumes that the fishing effort is uniformly distributed throughout the fishing season, can produce biased results in a fishery with strongly seasonal fishing effort (Sims 1982). We accommodated this fact by using a variant of MacCall's (1986) approximation that took the seasonal nature of the fishery into account. We used the VPA estimator:

$$\hat{N}_i = N_{i+1} \exp(M) + kC_i \qquad (2)$$

where $\hat{N}_i$ = the estimate of population (in numbers) at the start of year i,
C_i = the catch (in numbers) during year i,
M = the instantaneous rate of natural mortality (assumed constant),
k = a constant depending on M and the temporal distribution of catch throughout the year.

In most VPA applications, k is held constant. In contrast, we developed a procedure to find annual values of k fitting the distribution of each year's catch, which increased the accuracy of our population estimates. To do this, we performed an iterative monthly VPA on the unaged catch data, and found for each year the k_i that caused equation 2 to hold on an annual basis (MacCall 1986). These values of k_i were then used in the analysis of the aged annual catches by equation 2. Since the Pacific mackerel fishery is highly seasonal, this gave more accurate estimates of population number than did the standard iterative solution based on constant fishing effort over the full year.

Results of Virtual Population Analysis

The catch data after correction for underreporting are given in Table 2. The new VPA estimates of population number (Table 3) are slightly higher than the estimates of Parrish and MacCall (1978), especially in the years before 1940. This occurs because the correction for underreporting slightly outweighs the seasonal VPA correction in those years.

WEIGHTS AT AGE

The second data component used to estimate spawning biomass was the matrix of age- and year-specific weights at the nominal mean spawning date, May 1. This section describes our procedures for revising these weights for the years 1928–69 and 1974–84. Although spawning biomass estimates were not computed for the years 1974–84, weights for these years were needed to estimate earlier values.

The weight data fell into three groups: (1) no data for 1929 to 1938; (2) average weight of the season's catch by age for 1939 to 1969; (3) monthly weights at age beginning in 1977. Accordingly, we divided our analysis into the same three groups of years. For ease of narrative, we begin with the most recent period.

Years 1977–1984

Weights at age for each year, 1977–84, were based on monthly weight measurements of fish from the catch (R. Klingbeil, California Dept. of Fish and Game, unpubl. data). These were recorded from April through June of each year; we estimated May 1 weights as means of the recorded April and May entries (which, as monthly means, approximate mid-month weights). In years missing data from April or May, we assumed linear growth in weight during the season, interpolated the missing values, and took the mean of April and May

TABLE 2
Adjusted Catch Statistics for Pacific Mackerel in Numbers of Fish (Multiply by 1000)

Year	Age 1	Age 2	Age 3	Age 4	Age 5+
1929	12,743	23,027	21,338	5,338	9,073
1930	1,360	6,996	4,724	1,871	721
1931	942	9,834	6,093	1,287	1,310
1932	144	3,221	5,843	1,393	1,701
1933	4,162	17,132	28,727	21,048	11,286
1934	3,743	40,807	27,227	31,211	18,610
1935	8,468	9,921	48,061	49,709	33,609
1936	1,894	17,197	14,664	27,866	36,522
1937	1,414	2,484	7,701	15,249	36,690
1938	12,262	33,859	17,506	4,564	22,422
1939	30,304	31,916	42,246	12,711	13,757
1940	24,051	80,182	29,219	15,674	3,582
1941	15,093	31,924	30,967	6,180	1,833
1942	35,770	11,208	15,462	6,418	1,318
1943	15,378	66,767	12,532	8,802	1,822
1944	19,600	22,550	40,140	9,130	2,439
1945	16,941	12,233	12,152	12,216	5,681
1946	11,588	32,072	14,746	5,789	5,939
1947	1,867	10,816	14,831	6,894	4,839
1948	77,374	3,879	924	1,351	881
1949	26,987	60,924	5,292	851	1,102
1950	5,064	25,268	20,798	1,232	278
1951	1,920	5,371	16,825	13,497	451
1952	60	677	1,672	12,334	3,627
1953	1,102	774	951	262	1,237
1954	65,034	6,324	338	115	63
1955	6,986	41,490	11,806	400	278
1956	75,425	22,852	22,341	5,556	95
1957	7,273	35,604	13,234	9,530	3,871
1958	1,428	6,614	12,148	3,905	1,583
1959	62,281	4,618	1,151	1,407	612
1960	22,049	24,804	9,579	2,504	839
1961	35,576	18,143	12,934	2,719	381
1962	31,826	14,669	10,585	4,071	462
1963	4,042	23,458	13,626	8,315	1,272
1964	7,375	5,695	10,747	14,239	1,992
1965	1,321	801	1,777	5,772	10,698

weights as in other years. Values of w_{5+} were estimated as weighted means of weights at ages 5 and 6, namely

$$w_{i5+} = 0.8w_{i5} + 0.2w_{i6}$$

This ad hoc relationship was suggested by the relative frequencies of 5- and 6-year-old fish in the catch.

Years 1940–1968

For the 1939–69 seasons, publications of the California Department of Fish and Game tabulated each season's catches in weight and numbers by age (Fitch 1951, 1953a, 1953b, 1955, 1956, 1958; Hyatt 1960; Knaggs 1972; Parrish and Knaggs 1971, 1972). From these publications, each season's average (not May 1) weights w^*_{ij} at age were obtained by dividing catches in weight by catches in numbers. To estimate weights on May 1, we first calculated the mean harvest date of each fishing season from the monthly distribution of landings. We then assumed that the recorded mean weights at age occurred on that date. Finally, by assuming linear growth from one mean harvest date to the next, we estimated the May 1 weights at age (w_{ij}) by interpolation. Because 1939 was the first season with weight information, the first interpolation was for 1940. To estimate weights at age 5^+, we increased weights at age 5 by 5%, a value suggested by examining a few years for which both w_5 and w_{5+} were known.

The interpolation could not be done for age 1 in 1943 and 1945 because we lacked catch data for age 0, and for age 5 in 1954 because we lacked catch data for age 5. Therefore, these mean weights were estimated indirectly by referring to the relative weight of an adjacent cohort at the same age. For example, in 1953 the age 4 mean weight was approximately equal to the mean of age 4 weights in the preceding and following years; thus the age 5 mean weight in 1954 was estimated as the mean of

TABLE 3
Revised VPA Population Estimates of Pacific Mackerel in Numbers of Fish (Multiply by 1000)

Year	Age 1	Age 2	Age 3	Age 4	Age 5^+
1929	352,430	224,170	168,150	27,994	47,584
1930	754,120	204,480	119,190	86,449	33,317
1931	987,320	456,360	118,690	68,694	69,940
1932	1,094,400	598,120	269,220	67,294	82,159
1933	768,830	663,650	360,380	158,940	85,224
1934	276,090	463,280	390,010	197,600	117,820
1935	120,520	164,720	251,200	216,680	146,500
1936	151,650	66,824	92,559	116,750	153,020
1937	325,570	90,604	28,064	45,508	109,500
1938	237,380	196,400	53,076	11,199	55,014
1939	380,930	134,600	93,238	18,810	20,357
1940	246,870	206,630	55,927	22,517	5,146
1941	215,060	130,690	61,836	10,785	3,200
1942	458,450	118,680	54,396	13,380	2,747
1943	166,870	249,720	63,104	20,742	4,294
1944	150,350	89,142	99,071	28,440	7,597
1945	157,890	76,000	36,590	28,980	13,478
1946	47,175	82,465	36,491	12,651	12,979
1947	39,432	19,372	24,441	10,374	7,281
1948	396,570	22,498	3,527	3,548	2,316
1949	216,890	182,590	10,741	1,447	1,875
1950	24,255	111,590	65,693	2,601	588
1951	10,167	10,932	48,826	24,324	813
1952	6,226	4,737	2,630	17,082	5,023
1953	126,370	3,734	2,394	414	1,950
1954	311,330	75,759	1,641	686	378
1955	131,130	138,890	41,094	736	512
1956	229,670	74,130	52,130	15,787	269
1957	44,260	80,090	27,023	14,080	5,719
1958	67,801	21,210	20,994	6,137	2,488
1959	221,770	39,991	7,618	3,097	1,346
1960	192,800	85,817	20,645	3,721	1,247
1961	330,760	99,062	31,939	4,756	666
1962	168,500	173,080	46,041	9,360	1,063
1963	28,322	77,701	93,687	19,778	3,025
1964	16,632	14,205	29,875	46,802	6,546
1965	6,644	4,762	4,503	10,358	19,199

the preceding and following age 5 weights. A similar procedure was used for age 1 fish in 1943 and 1945; variations in relative weight of age 2 fish were used as the basis for comparison.

Years 1929–1939

Because no weight data had been collected, Parrish and MacCall (1978) had assumed that weights at age were constant before 1939. However, an examination of data from other years indicated that *Scomber japonicus* weights at age are quite variable, and appear to be density-dependent. The use of constant weights during a period of high abundance is likely to have produced biased estimates of spawning biomass.

To eliminate this source of bias, we estimated the 1929–39 May 1 weights at age by using linear regression models of known May 1 weights on May 1 abundances at age. The modeling procedure was similar for estimating weights at each age. (Although all weights are year-specific, the subscript for year is omitted below unless required for clarity.) The procedure for modeling w_1 was:

1. We computed all possible regressions of weight on population numbers of each age. (That is, $\hat{w}_{i1} = f(N_{i1} \ldots N_{i5})$.)
2. By examining goodness-of-fit statistics, including Akaike's information criterion (Akaike 1969), Mallows's C_p (Mallows 1964), and the R^2 and adjusted R^2 statistics (Kvålseth 1985), we chose one or two potential models from those computed for each age.
3. We plotted the selected models to examine goodness of fit and detect any possible outliers or other ill behavior.
4. Favoring simpler models, we chose one regression model and computed predicted values of w_1 where missing.

Models of w_2 through w_{5+} were constructed in a similar way, except that the weight of the same cohort at the previous age was included among the independent variables. For example, in predicting w_{i3}, we included $w_{i-1,2}$ among the possible regressors. In addition, we found it useful to include the same year's weight at the next younger age among the possible regressors. May 1 weights used for fitting the models were from the procedures described above for 1940–68 and 1977–84.

Special cases. The model for w_1 included N_2, which was unrecorded before 1926. Therefore no weight at age 1 was estimated for 1925. Similarly, the model for weight at age 2 included the population number at age 4, which was unrecorded before 1928. In order to estimate w_2 in 1927, we used a separate regression not including N_4. This made it possible to estimate w_3 starting in 1928, w_4 starting in 1929, and w_{5+} starting in 1930.

A value of w_{5+} for 1929 was necessary so that the year's data could be used for further analysis. A separate regression of w_{5+} on w_4 was used for 1929 only. This was possible because, for the older fish, the weights at age were correlated within a single year—in this case, Pearson's $r = 0.85$.

The w_{5+} value for 1965 (1.228), derived as discussed above through interpolation, was considered an outlier. The value of w_{5+} predicted from the regression model (1.495) was substituted for the interpolated 1965 value.

Results of Weight Analysis

The new series of estimated May 1 weights is given in Table 4. Equations for the regression models used to estimate pre-1939 weights are given in Table 5, with model statistics in Table 6. A plot of weight versus population size (Figure 1) illustrates the density-dependence in the stock.

FECUNDITIES AT AGE

Because of data limitations, we used estimated mean fecundities (m_j) that were not year-specific. This is similar to the methodology of Parrish and MacCall (1978), who used the following vector of age-specific fecundities, corresponding to age groups 1, 2, 3, 4, and 5^+:

$$m = \{\Phi_i, 0.77, 0.88, 1.0, 1.0\} \quad (3)$$

Here Φ_i, the fraction of age 1 biomass which is mature (m_{i1}), was the only year-specific element. It was given by:

$$\Phi_i = 0.54 \exp(-0.00717\, B^*_i) \quad (4)$$

where B^*_i is the total stock biomass, in millions of pounds, in year i.

This m vector was based on gonad observations from samples of the catch taken in 12 fishing seasons from 1958 through 1969 (Knaggs and Parrish 1973). Female mackerel gonads from those samples were classified into three categories: immature ("I," no eggs present); maturing ("g," eggs present); and mature ("G," large translucent eggs present). To derive the m vector, Parrish and MacCall combined the mean proportions of fish of each age falling into the g and G categories, which they considered to be equal indicators of maturity, and mul-

TABLE 4
Revised May 1 Weights (Pounds) at Age of Pacific Mackerel

Year	Age 1	Age 2	Age 3	Age 4	Age 5$^+$
1925	—	—	—	—	—
1926	0.396	—	—	—	—
1927	0.369	0.705	—	—	—
1928	0.348	0.613	0.918	—	—
1929	0.368	0.655	0.887	1.152	1.355
1930	0.306	0.664	0.931	1.127	1.330
1931	0.252	0.609	0.880	1.161	1.337
1932	0.178	0.611	0.836	1.121	1.332
1933	0.182	0.442	0.660	1.087	1.289
1934	0.313	0.436	0.513	0.950	1.186
1935	0.409	0.479	0.553	0.836	1.041
1936	0.425	0.626	0.745	0.867	0.998
1937	0.389	0.700	0.945	1.016	1.107
1938	0.383	0.683	0.988	1.172	1.284
1939	0.371	0.695	0.986	1.206	1.389
1940	0.429	0.575	0.795	0.984	1.280
1941	0.482	0.685	0.883	1.113	1.322
1942	0.381	0.703	0.900	1.143	1.465
1943	0.479	0.617	0.944	1.132	1.384
1944	0.461	0.739	0.903	1.182	1.422
1945	0.369	0.728	0.965	1.181	1.440
1946	0.411	0.654	0.966	1.204	1.423
1947	0.510	0.796	1.048	1.211	1.450
1948	0.351	0.741	1.060	1.275	1.484
1949	0.327	0.577	0.864	1.262	1.480
1950	0.462	0.564	0.804	1.059	1.437
1951	0.353	0.692	0.846	1.051	1.311
1952	0.611	0.785	1.058	1.213	1.442
1953	0.438	0.790	0.959	1.219	1.471
1954	0.342	0.740	1.075	1.227	1.484
1955	0.350	0.556	0.889	1.159	1.497
1956	0.398	0.652	0.899	1.092	1.403
1957	0.453	0.662	0.931	1.134	1.342
1958	0.413	0.697	0.844	1.093	1.294
1959	0.414	0.735	0.968	1.136	1.409
1960	0.364	0.690	1.044	1.285	1.521
1961	0.389	0.668	1.017	1.236	1.455
1962	0.508	0.751	1.039	1.236	1.480
1963	0.642	0.873	1.093	1.291	1.560
1964	0.576	0.827	1.119	1.312	1.616
1965	0.402	0.745	1.008	1.254	1.289
1966	0.371	0.717	1.070	1.292	1.715
1967	0.413	0.605	1.004	1.266	1.583
1968	0.427	0.712	1.051	1.240	1.524
1969	0.557	0.801	1.044	1.371	1.614
1970	—	—	—	1.250	1.524
1971–74 No data					
1975	0.465	—	—	—	—
1976	0.465	0.741	—	—	—
1977	0.415	0.940	1.840	—	—
1978	0.473	0.880	1.730	1.920	2.221
1979	0.195	0.865	1.255	1.715	2.205
1980	0.230	0.420	1.010	1.340	1.732
1981	0.265	0.610	0.650	1.250	1.537
1982	0.210	0.500	0.660	0.860	1.357
1983	0.300	0.520	0.745	1.010	1.222
1984	0.300	0.455	0.690	0.855	0.991

tiplied the resulting m vector by a constant α to scale k_5 to unity.

$$m_j = \alpha\{P_j(g) + P_j(G)\} \qquad (5)$$

where m_j = the estimated mean proportion mature at age j.

α = the scaling constant described above,

$P_j(g)$ = the fraction of fish of age j in classification g,

$P_j(G)$ = the fraction of fish of age j in classification G.

TABLE 5

Regression Models of Pacific Mackerel Weights at Age[a]

$$\hat{w}_{t1} = 0.469 - 0.000208N_{t1} - 0.000252N_{t2}$$

$$\hat{w}_{t2} = 0.166 + 0.651w_{t1} + 0.585w_{t-1,1} + 0.000243N_{t1} - 0.00087N_{t4}$$

$$\hat{w}_{t3} = -0.313 + 1.055w_{t2} + 0.829w_{t-1,2}$$

$$\hat{w}_{t4} = 0.435 + 0.780w_{t-1,3}$$

$$\hat{w}_{t5+} = 0.122 + 0.613w_{t4} + 0.544w_{t-1,4}$$

[a] Subscripts refer to year and age, in that order. Symbols are defined in the text.

TABLE 6

Statistics from Regression Models of Pacific Mackerel Weights at Age

Weight estimated	n	Adjusted R^2	F statistic	Prob. of larger F
w_{t1}	35	0.443	14.9	< 0.0001
w_{t2}	35	0.79	33.4	< 0.0001
w_{t3}	35	0.63	30.4	< 0.0001
w_{t4}	34	0.89	282	< 0.0001
w_{t5}	33	0.84	89.0	< 0.0001

Recent histology by Dickerson and Macewicz[2] indicates that the three gonad classifications have a different interpretation from that of Parrish and MacCall. Examination of gonads taken during the 1985 spawning season showed that the G category represented hydrated eggs, indicating spawning imminent within a few hours, whereas the g category was the normal state of mature, spawning fish. Dickerson and Macewicz also report that, in the 1985 spawning season, the average mature female's mean spawning frequency was about once per 12 days, while fish at maximum egg production spawned approximately once per 1.3 days. We assumed that fish in category g were average mature females, and that those in category G were at maximum egg production. (This interpretation, although it may not be accurate, appears better than the previous assumption that g and G represent equally important indicators of maturity.) This leads to a new expression, replacing equation 5, for establishing the m vector, and a new interpretation; i.e., that m_j reflects relative fecundity, not just maturity, at age. The new expression is:

$$m_j = \frac{P_j(\mathrm{g})}{12} + \frac{P_j(\mathrm{G})}{1.3} \tag{6}$$

where m_j = the new relative fecundity index for age j,
$P_j(\mathrm{g})$ = the fraction of fish of age j in classification g,
$P_j(\mathrm{G})$ = the fraction of fish of age j in classification G.

Equation 6 allowed us to reevaluate the m vector (equations 3 and 4) established by Knaggs and Parrish (1973); their original data were kindly provided us by Richard Klingbeil (Calif. Dept. of Fish and Game, Long Beach, pers. comm.). The 12 years of data were tabulated by the five age groups (1 through 5^+) and eight months (March through October) in which spawning tends to occur. Of these 480 cells, only 280 contained data, of which 86 were zero observations; thus, only 40% of the cells contained nonzero values for m.

We postulated a model in which multiplicative year and age parameters produce a predicted value for the annual spawning output, defined as the sum of the monthly cells for the year. The age factors of this model form the m vector. Although the model could have been fit directly to the data by maximum likelihood, the effort for that approach exceeded our resources, so we chose instead to estimate parameters by analysis of variance (ANOVA) of log-transformed data. To remove month effects, we conducted the ANOVA on yearly sums.

It was necessary to fill missing cells before computing the yearly sums. To accomplish this, we used a second ANOVA based on additive year, month, and age effects to estimate values for the empty cells. This ANOVA was weighted according to the square root of the number of observations in each cell. (Independence of data would warrant weighting by the number of observations; however, the samples of fish came from schools, within which spawning condition was probably corre-

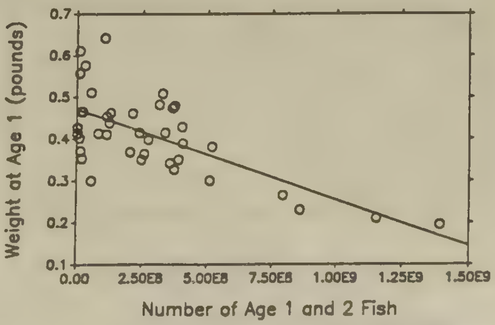

Figure 1. Density-dependence of weight at age 1 in the Pacific mackerel stock. Data shown cover years 1940–84, and do not include weights estimated by regression analysis. The regression line is shown for illustration. Other ages are similar.

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[2] Dickerson, T. L., and B. J. Macewicz. MS. Spawning frequency and batch fecundity of chub mackerel, *Scomber japonicus*, during 1985. Available from B. J. Macewicz, Southwest Fisheries Center, P. O. Box 271, La Jolla, CA 92038.

lated. By means of the square root weighting, we attempted to acknowledge this fact while also recognizing that larger sample sizes should nonetheless provide more precise index values.) Very large *F* statistics from this ANOVA suggested that year, month, and age effects were all meaningful; however, lack of normality, the nonstandard weighting scheme, and the additive model, which is probably misspecified, prevented computation of parametric significance probabilities.

After empty monthly cells were replaced by predicted values, the yearly sums formed a data matrix of 12 years by five ages. Negative values in this matrix were treated as missing values. Because abundances from 1966 to 1969 were the lowest on record, and spawning activity the highest, these years were deleted as possibly reflecting an atypical level of spawning activity. Data from 1958 and 1965 were also deleted, because their yearly indices were based on fewer than seven actual (i.e., not estimated) monthly values. The six-year period from 1959 to 1964 remained as the data available to estimate the age specific *m* vector.

Results of Fecundity Analysis

The model of year and age effects was estimated by ANOVA of log-transformed values with equal cell weights. Large *F* values, although not strictly statistically significant, indicated likely biological significance. Exponentiating the age effects from the ANOVA gave an *m* vector of:

$$m = \{0.0586, 0.4837, 0.9107, 0.9118, 1.0\} \qquad (7)$$

Because the age 3, 4, and 5^+ elements of equation 7 were all very similar, we averaged them and rescaled them to unity. This gave a final *m* vector of

$$m = \{0.062, 0.514, 1.0, 1.0, 1.0\} \qquad (8)$$

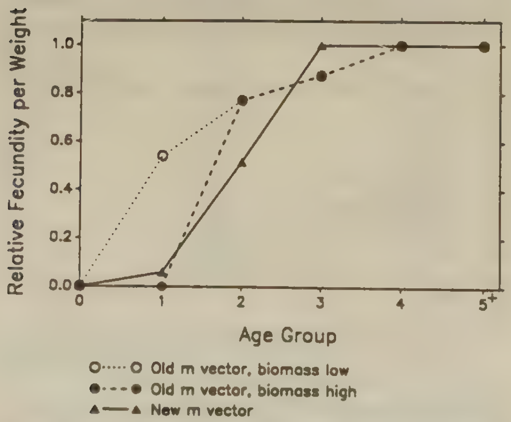

Figure 2. Spawning ogives under new and revised fecundity schedules (*m* vectors). The new schedule reveals that spawning is more concentrated among the older ages.

We found little evidence of density-dependent changes in m_1. Its small magnitude supports Fry's (1936) observation that yearling fish do not spawn.

In view of the new fecundity schedule (*m* vector), it appears that Parrish and MacCall overestimated the contributions of ages 1 and 2 to egg production, even though it was correct that relatively large fractions of these age groups were mature and capable of spawning. The new schedule shifts the spawning biomass to a slightly older mean age, as illustrated in Figure 2, which gives spawning ogives under the old and new *m* vectors.

Figure 3 compares eggs-per-recruit (EPR) curves (fecundity multiplied by survivorship; Prager et al. 1987) for unexploited and exploited populations under old and new schedules, given fishing availabilities from MacCall et al. (1985). The EPR curves with no fishing were scaled to unity; exploitation was at $F = 1.0$; Φ_i was set to 0.26, an average

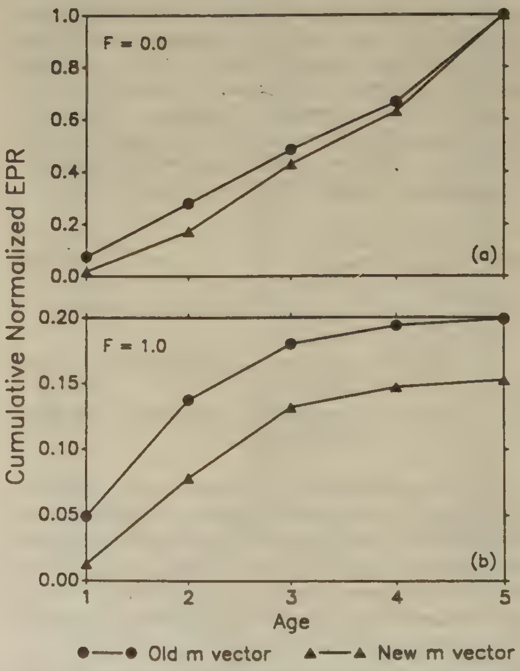

Figure 3. Cumulative eggs-per-recruit (EPR) curves for the Pacific mackerel stock under old and new fecundity schedules (*m* vectors). Curves have been normalized so that each yields EPR = 1.0 with no exploitation. (*a*), Unexploited stock; (*b*), stock exploited at annual $F = 1.0$.

value, for the old *m* vector. With exploitation, the new cumulative EPR curve reaches 0.15, whereas the old curve reaches 0.20. In other words, at $F = 1.0$, spawning output is about 75% of what we thought under the old schedule; thus, slightly less harvestable productivity might be expected. Certainly, these results suggest that the population's spawning productivity is more affected by fishing than was previously believed.

SPAWNING BIOMASS ESTIMATION

The final spawning biomass estimates (Table 7) are presented with approximate 95% confidence intervals in Figure 4. The standard deviation of the estimates was computed by the delta method (Seber 1973; Prager and MacCall 1988); we assumed a 5% coefficient of variation on each element of the *m* vector; confidence intervals were computed as ± 2 standard deviations. Figure 5 presents the old (Parrish and MacCall 1978) and new (this paper)

TABLE 7

Revised Spawning Biomass Estimates for Pacific Mackerel in Pounds (Multiply by 1000)

Year	Spawning biomass	Std. deviation of sp. biomass	Coefficient of variation
1929	329.400	308.350	93.6%
1930	336.800	299.583	89.0%
1931	435.900	318.591	73.1%
1932	609.800	370.675	60.8%
1933	679.900	344.674	50.7%
1934	636.700	277.471	43.6%
1935	516.100	192.120	37.2%
1936	348.400	114.978	33.0%
1937	234.400	67.535	28.8%
1938	210.700	53.703	25.5%
1939	199.700	46.787	23.4%
1940	140.800	17.804	12.6%
1941	123.300	21.347	17.3%
1942	122.000	29.215	23.9%
1943	173.100	35.539	20.5%
1944	172.000	30.077	17.5%
1945	121.000	20.888	17.3%
1946	97.870	13.122	13.4%
1947	57.910	6.829	11.8%
1948	28.900	6.046	20.9%
1949	72.430	11.925	16.5%
1950	89.460	14.244	15.9%
1951	72.050	9.346	13.0%
1952	32.890	3.986	12.1%
1953	10.620	2.858	26.9%
1954	38.580	9.596	24.9%
1955	80.690	13.513	16.7%
1956	94.990	12.919	13.6%
1957	77.290	8.817	11.4%
1958	36.980	4.969	13.4%
1959	33.590	6.777	20.2%
1960	63.020	10.635	16.9%
1961	81.320	18.218	22.4%
1962	133.100	34.943	26.3%
1963	168.600	36.878	21.9%
1964	112.000	19.593	17.5%
1965	44.270	5.828	13.2%

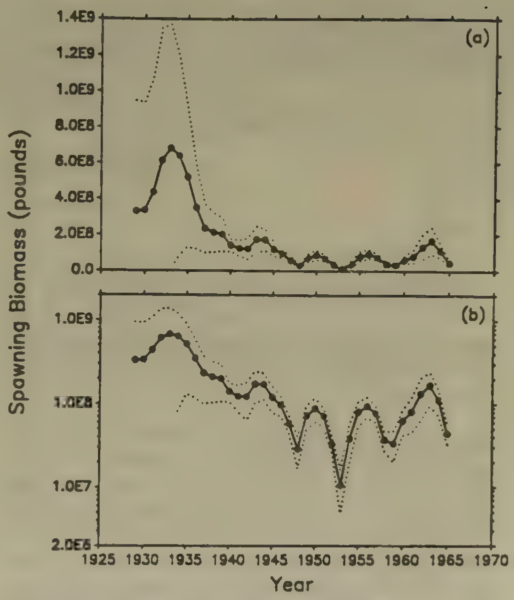

Figure 4. Revised spawning biomass estimates for Pacific mackerel stock, with approximate 95% confidence interval (*dotted line*). (*a*), Linear scale; (*b*), log scale. Large confidence bounds before 1940 reflect less precise knowledge of age structure and weights at age.

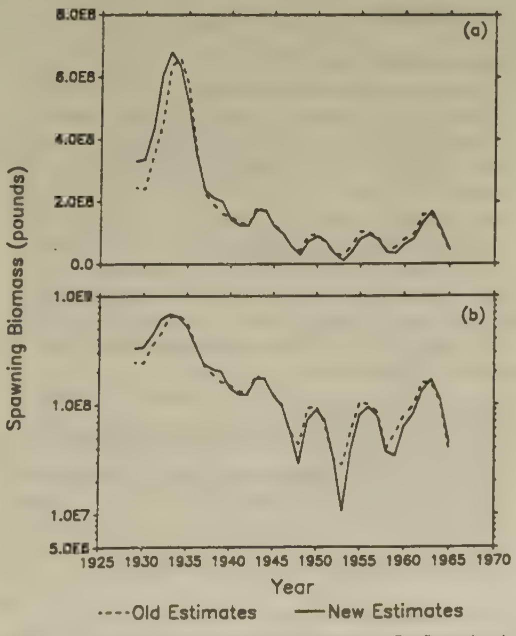

Figure 5. Old and revised spawning biomass estimates for Pacific mackerel stock: (*a*), linear scale; (*b*), log scale.

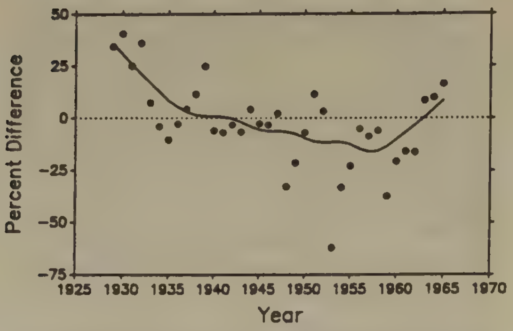

Figure 6. Difference between old and revised spawning biomass estimates, expressed as percent difference from the old to the new estimate [i.e., (old − new) × 100 / old]. Smoothed line is locally weighted robust regression (LOWESS).

spawning biomass estimates. Although they appear quite similar, a closer look presents a different picture. Figure 6, which shows the differences (between new and old estimates) as percentages of the old estimates, illustrates that the declining trend of the spawning biomass from 1925 to 1962 is more clearly seen under the new estimates. This clearer vision is a direct result of increased knowledge of the Pacific mackerel's spawning biology. We hope that our clearer view of the stock's population dynamics will help to lessen the probability of another collapse.

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Sensitivities and Variances of Virtual Population Analysis As Applied to the Mackerel, *Scomber japonicus*

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Prager, M. H., and A. D. MacCall. 1988. Sensitivities and variances of virtual population analysis as applied to the mackerel, *Scomber japonicus*. Can. J. Fish. Aquat. Sci. 45: 539–547.

Virtual population analysis (VPA) is widely used in fish stock assessment. However, VPA results are generally presented as point estimates, without error variance. Using numerical methods, we estimated the total variance of historical (1929–65) biomass estimates of mackerel, *Scomber japonicus*, off southern California. In the years before 1940, coefficients of variation (CV's) approached 100%; later, when weights at age and the age structure of the catch were better known, the CV's were about 25%. Most of the variability derives from uncertainties in estimates of natural mortality (*M*) and of weights at age. We also developed dimensionless coefficients (sensitivities) to examine the effects of errors in the inputs on the VPA biomass estimates. The largest sensitivities were to *M* and the total catch and varied substantially from year to year. As expected, sensitivity to *M* decreased with increasing exploitation, and sensitivity to catch increased with increasing exploitation. Using such sensitivities, one could estimate the error in a biomass estimate for a past year when *M* (or any other input) was thought to be unusually high or low. Thus, retrospective corrections can be made. Also, such sensitivities form an analytic tool for examining the properties of VPA, or any quantitative model.

L'analyse de population virtuelle (APV) est largement utilisée pour l'évaluation des stocks de poissons. Les résultats de cette analyse sont généralement présentés comme des estimations ponctuelles, sans erreur de variance. Les auteurs ont estimé par méthodes numériques la variance totale, de 1929 à 1965, des estimations de biomasse de maquereau, *Scomber japonicus*, au large du sud de la Californie. Au cours des années antérieures à 1940, les coefficients de variation (CV) étaient presque de 100 % tandis que plus tard, lorsque l'on a mieux connu les poids selon l'âge et la structure des âges des prises, les valeurs de CV étaient de 25 % environ. La plus grande partie de la variabilité découle d'incertitudes liées aux estimations de la mortalité naturelle (*M*) et du poids selon l'âge. Les auteurs ont aussi déterminé des coefficients sans dimension (de sensibilité) afin d'étudier les effets des erreurs des paramètres d'entrée sur les estimations de biomasse par APV. Les éléments de sensibilité les plus importants avaient trait à *M* et aux prises totales et variaient de façon appréciable d'une année à l'autre. Tel que prévu, la sensibilité à la valeur de *M* diminuait à mesure que le taux d'exploitation augmentait et celle aux prises augmentait en même temps que le taux d'exploitation. Ces éléments de sensibilité pourraient permettre d'estimer l'erreur d'une biomasse estimée pour une année antérieure lorsque la valeur de *M* (ou de tout autre paramètre d'entrée) apparaît anormalement élevée ou faible. Il serait donc possible d'apporter des corrections a posteriori. De plus, ces éléments de sensibilité constituent un outil analytique pour l'examen des propriétés de l'APV ou de tout autre modèle quantitatif.

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Virtual population analysis (VPA) has been applied widely to commercial fish stocks in the more than 20 yr since its development (Murphy 1965; Gulland 1965). Although several studies have examined the errors implicit in the method, VPA abundance estimates still tend to be presented as exact numbers, i.e. without error variances. Pope (1972) examined separately the effects of error in the estimate of terminal instananeous fishing mortality (*F*) and of errors in the catch statistics. Sims (1982) examined the errors caused by assuming a constant fishing effort throughout the fishing season, in the presence of seasonal variation in effort. Saila et al. (1985) discussed the propagation of error in Pope's (1972) approximation (and therefore the basic model). However, none of the above authors discussed the effects of simultaneous errors in several parameters, nor of covariances among the parameters. Sampson (1984) overcame these limitations for analysis of a single cohort. However, the cited studies have stopped short of estimating the variances of VPA abundance estimates themselves.

We used the delta method (Seber 1973) to examine the errors caused by simultaneous errors in any number of parameters, including covariances, and have applied the method to the southern California stock of mackerel, *Scomber japonicus*. Our work provides a numerical estimate of the variance of each year's biomass estimate. In addition, we have developed a method to examine the sensitivity of VPA to its input parameters.

The California fishery on *S. japonicus*, known locally as Pacific mackerel and elsewhere as chub mackerel, supported a commercial fishery from the late 1920's to the mid-1960's (Parrish and MacCall 1978). The resource was severely depleted during the following decade, but recovered strongly in the late 1970's, when it reached record levels of abundance (MacCall et al. 1985). As the fishery is monitored closely by the California Department of Fish and Game, continuous landings and age composition data are available except for the years 1970–75, when landings were insufficient to support the monitoring effort. We used the data collected from 1920 to 1969 as the basis for the present study. The data collection and subsequent analysis are described in detail in Parrish and MacCall (1978), MacCall et al. (1985), and Prager and MacCall (1987).

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Methods

Cohort Analysis

To compute population estimates, we used a variation of MacCall's (1986) approximation, which can be stated in the form

$$(1)\quad N_t \approx N_{t+1}\exp(M) + kC_t$$

where N is the population estimate in numbers, M is natural mortality, C is the catch, the subscripts t and $t + 1$ represent relative time in years, and k is a constant whose value depends on M and on the temporal distribution of the catch throughout the year. MacCall suggested using

$$(1a)\quad k = M/\{1 - \exp(-M)\}$$

as an improvement over Pope's (1965) approximation. However, to maximize the accuracy of our VPA, we calculated a value of k based on an iterative monthly VPA on the unaged monthly catch data so that equation 1 holds on an annual basis. These year-specific values of k were then used in the analysis of the aged annual catches. Since the Pacific mackerel fishery is highly seasonal, MacCall's approximation (MacCall 1986) is more accurate than the iterative solution by annual VPA, even when equation 1a is used without fitting k to the seasonal distribution of catch.

Equation 1 estimates age-specific abundances in numbers; biomass estimates are obtained by multiplying equation 1 by the respective weights at age. The stock's total biomass B in year i is estimated as the sum of the age-specific biomasses (for ages $1 \ldots m$) at the beginning of the fishing season, i.e.

$$B_i = \sum_{j=1}^{m} w_{ij}\cdot N_{ij}.$$

Murphy's Linkage Algorithm

Estimation of terminal fishing mortality rates is one of the largest difficulties in performing VPA. Murphy (1965) described an objective method of estimating terminal F by linking cohorts. This method has been used in the previous VPA's of the Pacific mackerel stock (Parrish and MacCall 1978; MacCall et al. 1985). Murphy's linkage method requires only one estimate of terminal F to start the analysis of any number of contiguous cohorts. The method as used in this fishery comprises the following steps (Fig. 1): (1) Estimate the terminal F for the oldest age-class (5$^+$) in the final year (t), where the notation 5$^+$ indicates all fish aged 5 and older. (2) Calculate $N_{t,5}{}^+$ in the final year from $C_{t,5}{}^+$ and $F_{t,5}{}^+$. (3) Use VPA to estimate $N_{t-1,4}{}^+$ and $F_{t-1,4}{}^+$. (4) Since the mackerel is considered fully recruited at age 4, assume that in each year $F_5{}^+$ is equal to $F_4{}^+$. (5) This value of $F_{t-1,5}{}^+$ supplies a new terminal fishing mortality rate for VPA estimation of $F_{t-2,4}{}^+$. By repeating steps 3, 4 and 5 for each earlier year, an estimate of $F_4{}^+$ for each year is obtained. (6) Assume that $F_4 = F_4{}^+$ in each year. From this value of F_4, calculate N_4 and perform a standard backwards VPA for the cohort from age 4 back to age 1. A key assumption of Murphy's linkage algorithm is that fishing mortality is the same among fully recruited age-classes. Thus, in each year, it is presumed that

$$(2)\quad F_4 = F_4{}^+ = F_5{}^+.$$

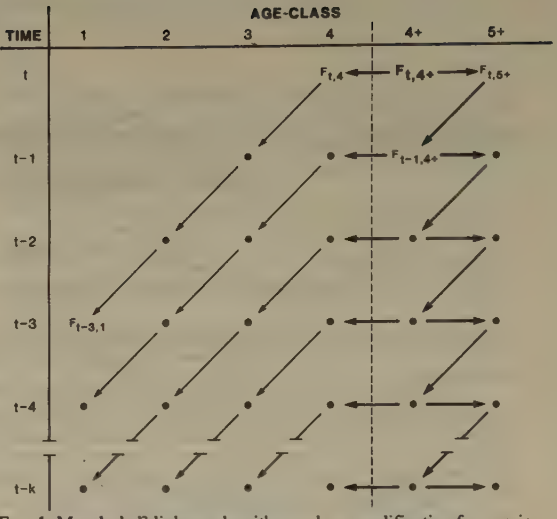

FIG. 1. Murphy's F-linkage algorithm and our modification for a series of $k + 1$ yr is illustrated by a matrix of F values. (For clarity, most are represented by dots.) The algorithm starts at the top with $F_{t,4}{}^+$, and first follows all bold arrows diagonally and horizontally. Then, the algorithm completes all paths shown by the lighter arrows. Diagonal arrows represent calculation of F values by backwards VPA. Horizontal arrows to the right represent transfer of F values by the F transfer coefficient (FTC, equation 3) or by equality in Murphy's original algorithm. Horizontal arrows to the left represent transfer of F values by equation 5 (or by equality in the original algorithm). The bold paths yield an estimate of F_4 for each year. The light paths complete the biomass estimates.

F Transfer Coefficient

We relaxed the assumption of equation 2 by postulating that $F_5{}^+$ is proportional, but not necessarily equal, to $F_4{}^+$ because of fluctuations in availability among ages and years. Varying differential growth, for example, could cause such fluctuations. The values of $F_4{}^+$ are assumed known from VPA. Then for each year, the estimate of $F_5{}^+$ is

$$(3)\quad F_5{}^+ = F_4{}^+ \cdot \mathrm{FTC}$$

where FTC is a transfer (proportionality) coefficient. In practice we consider FTC to be stochastic, with mean 1.0. In other words, Murphy's linkage (equation 2, which implies FTC of unity) is assumed to be valid only on average.

By parameterizing the FTC in this way, we can assume a nonzero variance σ^2_{FTC} for the relationship between $F_4{}^+$ and $F_5{}^+$ (which leads to a similar relationship between $F_4{}^+$ and F_4) and examine the effect that this variability has on the VPA population estimates. The approach also allows exploration of mean

FTC values other than unity; in this study, we examined values of 1.0, 0.9, and 1.25.

For a given F_4^+ and FTC, F_4 can be calculated by noting the relationship

$$(4)\quad a_4 = \frac{C_{4^+} \cdot a_{4^+} - C_{5^+} \cdot a_{5^+}}{C_4}$$

where a_i is defined as the reciprocal of the exploitation rate:

$$(4a)\quad a_i = Z_i/\{F_i \cdot [1-\exp(-Z_i)]\}.$$

Substituting equation 4a into 4 and solving for F_4, we obtain

$$(5)\quad F_4 = M/\{a_4\,[1 - \exp(-F_4 - M)] - 1\}.$$

Although equation 5 cannot be solved analytically, it can be solved easily by iteration. We used F_4^+ as a starting estimate of F_4 and obtained convergence in a few iterations.

Murphy's linkage algorithm resembles schemes of "separable VPA" (Doubleday 1976; Deriso et al. 1985). Separable VPA estimates relative availabilities at age, which are used to predict age-specific estimates of fishing mortality as a combination of independent age- and year-specific factors. Terminal F values for adjacent cohorts are linked by optimizing the fit to this model. Murphy's algorithm does not attempt to extend this rationale to partially available ages, but focuses only on fully available ages. Murphy's use of combined cohorts increases sample sizes, and thereby reduces this source of random variability. However (as in Gulland's VPA), no degrees of freedom remain, so his algorithm leaves no direct means of accounting for stochastic variability in the model, unlike separable VPA. Our treatment attempts to reintroduce considerations of stochasticity into the linkage. At the same time, it provides a method of extending Murphy's linkage algorithm to the case of unequal availability.

Variance Estimation

To estimate the variances of the VPA biomass estimates, we used the delta method (Seber 1973). The delta method numerically estimates the variance of a function $B(x_1, x_2, \ldots, x_r)$ by means of a Taylor expansion. The expression for the estimated variance of B is

$$(6)\quad \mathrm{Var}[B(x)] \approx \sum_{k=1}^{r} \mathrm{Var}[x_k] \cdot (\partial B/\partial x_k)^2 + 2 \sum_{k<l}\sum \mathrm{cov}[x_k, x_l] \cdot (\partial B/\partial x_k) \cdot (\partial B/\partial x_l).$$

In this case, the function B is the population biomass estimate and the x_k (and x_l) are the usual data needed for a VPA estimate of stock biomass: the catches and weights at age in each year, the natural mortality coefficient M, an estimate of the fishing mortality coefficient in the final year (terminal F), and, in our application, the FTC.

To solve equation 6 for Var[B], one must estimate the variances of each x_k, the covariances of each pair of x_k, x_l, $k \neq l$, and the partial derivatives of B with respect to each x_k. Where possible, we made these estimates based on data or theoretical grounds, but were forced to make ad hoc assumptions in several cases because of lack of data.

Partial Derivatives

We used numerical derivatives for the $\partial B/\partial x_k$. To calculate them, we made a cohort analysis estimate of stock biomass B_1 for a given year. Then the x_k being considered was temporarily increased by 1% and a new stock biomass estimate B_2 was made. By definition:

$$(7)\quad \partial B/\partial x_k \approx (B_2 - B_1)/0.01x_k.$$

Variances of Catches at Age

For most of the period under consideration, samples of mackerel from the catch were aged by examining the otoliths, and the age composition of the total catch was computed using a stratified estimate with monthly strata (Fitch 1951). As an example, let us assume that of the n_i fish aged in year i, the proportion falling into age-class j was p_{ij}. As the proportions in the different age-classes are distributed multinomially, the sampling variance of each p_{ij} is given by

$$(8)\quad \mathrm{Var}[p_{ij}] = p_{ij} \cdot q_{ij}/n_i$$

where $q = (1 - p)$. Since the *monthly* age composition data had been lost, we assumed that the age composition of the total catch was the same as that of the sample, i.e. that

$$(9)\quad C_{ij} = C_i \cdot p_{ij}$$

where C_i is the total catch in year i. Then the variance of C_{ij} is given by

$$(10)\quad \mathrm{Var}[C_{ij}] = C^2_i \cdot \mathrm{Var}[p_{ij}] = C^2_i \cdot p_{ij} \cdot q_{ij}/n_i.$$

In the years before 1933 and between 1935 and 1938, age composition of the catch was determined by modal analysis of the length–frequency histogram, rather than by otolith ageing (Parrish and MacCall 1978). This introduced two problems. First, the numbers of fish measured in these years are not known. And second, because the method is not particularly accurate, the ageing variance Var[C_{ij}] for these years is higher than the nominal estimated value (equation 10) by an unknown amount. We incorporated both of these phenomena in an admittedly ad hoc way. First, we found the smallest proportion (n_i/C_i) of fish sampled for otolith analysis in any year. Then, for the years of modal analysis, we used for each n_i (the number of fish sampled) in equation 10 this proportion times the year's catch divided by 2. For given proportions at age, this resulted in twice the estimated variances for C_{ij} in those years.

Variance of Total Catch

Equation 10 estimates the variance in each C_{ij} due to sampling error of the proportions. However, the variance of C_{ij} is further increased by any uncertainty in the estimate of total catch for the year, C_i. We treated this source of variability separately by assuming for each C_i a coefficient of variation of 5%, a value believed to approximate the uncertainty in the official catch records (R. Klingbeil, California Department of Fish and Game, 245 W. Broadway, Long Beach, CA 90802, USA, pers. comm.).

Variances and Covariances of Weights at Age

As the weight at age data are derived by two different methodologies, we used different approximations to estimate the variances and covariances of the estimated mean weights at age.

1940 to 1968

Mean weights at age for the fishing season were known (Fitch 1951), but no information on variance was available. Estimated

May 1 weights were estimated by Prager and MacCall (1987) from the published mean weights by linear interpolation based on the mean dates of each year's catch.

Estimation of the variances associated with those weight estimates posed several problems. First, variance arises from sampling errors and changes in timing of the fishery, as well as from estimation errors in the interpolations. Also, one expects covariance among weights of different ages within a season, as all are likely to be high or low together. These covariances must be known to compute the variance of the biomass estimate (equation 6).

To estimate the variance for each weight at age, a 3-yr centered moving average W^*_{ij} of the estimated May 1 weights was used as a plausible estimate of the true weight at age for that year. The deviation of the year's estimate from the 3-yr mean is called d_{ij}. Then, d_{ij} divided by the 3-yr mean provides a standardized deviate (STD) for that year:

$$\mathrm{STD}_{ij} = W^*_{ij}/d_{ij}.$$

The variance–covariance (STDCOV) matrix of these standardized deviates was used to estimate the variances and covariances of the estimated weights at age. The estimated covariance for the two ages j and k in year i is

$$(11)\quad \mathrm{Cov}[W_{ij},W_{ik}] = \mathrm{STDCOV}_{jk}\cdot W_{ij}\cdot W_{ik}$$

where variance is the special case of $j = k$. In effect, the values in the STDCOV matrix are squared coefficients of variation.

Pre-1940

Because no weight data exist, the weights at age before 1940 were estimated by regression analyses on population size. In some cases the weights of adjacent ages were included in the regression models (Prager and MacCall 1987). The STDCOV matrix developed for the 1940–68 weights at age was assumed to apply to these estimates as well. The regression models used to reconstruct the weights introduced additional error, and by the sequential nature of the reconstruction, these errors propagated from younger to older ages. On the other hand, weight estimates for the older ages used information from adjacent ages or cohorts, thus averaging out some of the error. The error of the regression model for weight of age 1 fish suggests a coefficient of variation (CV) of about 20%. The mean-squared error is 1218 g^2, and the mean weight is 177 g; thus the coefficient of variation is

$$(12)\quad \mathrm{CV} = (1218)^{1/2}/177 = 0.197$$

or about 20%. Although the models of older ages appear to have higher R^2, this is misleading, since those models rely upon the estimated weights at previous ages.

To accommodate these facts, we assumed that each reconstructed weight should have its variance inflated by 20% to reflecting a constant and independent 20% reconstruction error. This was accomplished by increasing all values in the STDCOV matrix by 0.04 before applying equation 11 to compute variance for the pre-1940 data. Because each age's variance is assumed to be independent, and the biomass estimates were composed of five ages, some of this additional variance canceled out in the computations.

Variance of the Natural Mortality Coefficient, M

We know of no publication in which an estimate of the variance of M has been derived for any fish stock. We regrettably cannot provide the exception and have estimated this quantity in an ad hoc manner, although the estimate is strengthened by theoretical considerations. The estimate of M (0.50/yr) for *S. japonicus* is taken from Parrish and MacCall (1978).

Before estimating the variance of M, we considered that it might arise from two sources. The first source is *measurement error*, our inability to measure the mean of M precisely. As our VPA uses a single estimate of M for all years (as do all VPA methods we are aware of), any measurement error affects all years of the analysis simultaneously. This means that, to model measurement error, only one partial derivative with respect to M must be computed for each year's biomass estimate (B_i).

The second source of variance in M is *process error*, the year-to-year variability in a quantity (M) not estimated every year. Although process error can be autocorrelated, we assumed the simplest case, i.e. that process error would affect the value of M in each year of the analysis independently. To model such process error, one must compute for each year's biomass estimate a separate partial derivative with respect to M for each year whose data contribute to the biomass estimate.

We assumed for simplicity that the contributions of the two sources to the variance of M were equal. For computational purposes, then, we split M into two equal components: a "low-frequency" component (subject to measurement error) and a "high-frequency" component (subject to process error). The variance of M was divided between the two components, also. Thus, we write

$$(13)\quad M = M_0 + M_1.$$

Here, M_0 is the low-frequency component of natural mortality, i.e. the component whose variance, arising from measurement error, affects all years at once. In contrast, M_1 is the high-frequency component, i.e. the component whose variance, arising from process error, affects each year separately.

We estimated M to have a coefficient of variation of about 25%, i.e. we believed a 95% confidence interval from M = 0.25 to M = 0.75 to be approximately correct. This gives an estimated variance of 0.0156, which we rounded to 0.016. To explore the implications of the two sources of variance in M, we repeated our analysis for three scenarios: the first had all the variance (0.16) in M_0, the second had all the variance in M_1, and the third had the variance divided equally between them.

Variance of Terminal F

The required estimate of the terminal F ($F_4{}^+$ in 1969) was set at 1.0 (Parrish and MacCall 1978), with estimated variance of 0.5. The estimated variance, while somewhat arbitrary, does reflect the variance found in the distribution of fishing mortality values observed over the years (Parrish and MacCall 1978; MacCall et al. 1985); it also reflects our opinion of the uncertainty in this estimate of F. Because we used Murphy's linkage method, the value of terminal F was much less important than in nonlinked cohort analyses.

Covariances

Except as explained above for the weights at age, covariances among the VPA input quantities were not calculated directly. We assumed that the covariances between different quantities (e.g. $\mathrm{Cov}[F,M]$ or $\mathrm{Cov}[w_i, C_i]$) were zero. Since the catches at age were treated as proportions, their covariances within a given year would be negative. This fact was treated numerically, while

TABLE 1. Index to VPA biomass and variance estimates, identified by computer run number. M_0 is the component of natural mortality whose variance acts on all years together; M_1 is the component of natural mortality whose variance acts on each year independently (equation 13). Run 22 is used in the text as the base for comparisons.

Run number	M_0 mean	M_0 variance	M_1 mean	M_1 variance	FTC mean
20	0.5	0.016	0.0	0.0	1.0
21	0.0	0.0	0.5	0.016	1.0
22	0.25	0.008	0.25	0.008	1.0
23	0.25	0.008	0.25	0.008	1.25
24	0.25	0.008	0.25	0.008	0.9

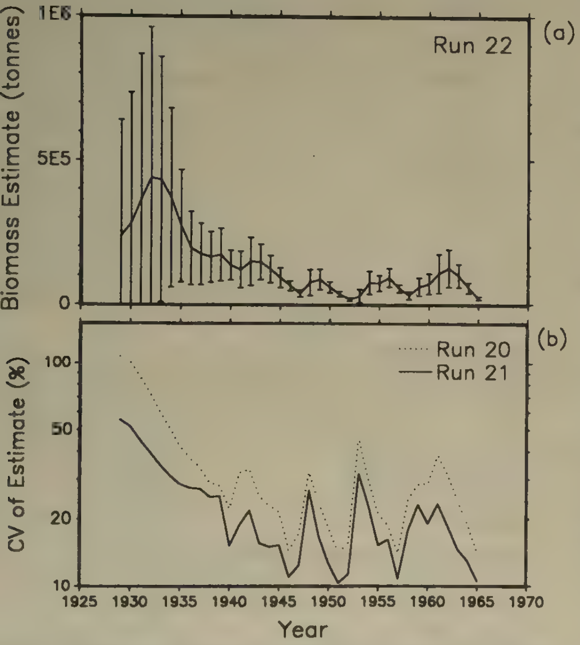

FIG. 2. Biomass and variance estimates for the mackerel, *Scomber japonicus*. (a) Biomass estimates with approximate 95% confidence intervals from run 22; (b) coefficients of variation (CV's) of biomass estimates from runs 20 and 21. CV's from run 22 were in between, somewhat closer to run 20. Runs differ in their assumptions about the variance of natural mortality (Table 1).

estimating the partial derivatives (equation 7) of catch at age, by taking the temporary 1% increase in each C_{ij} from the other catches in the same year. When C_{ij} was temporarily increased by 1%, the other catches were temporarily reduced (in proportion to their contribution to the total catch for the year) so that the total catch remained the same. Thus, although few of the covariance terms in equation 1 were computed explicitly, most of the covariances were taken into account.

Sensitivity Factors

During the analyses, it became apparent that the partial derivatives of the biomass estimate with respect to the input quantities ($\partial B_i/\partial x_k$), which were computed to accomplish the delta method, were of interest as indicators of the sensitivity of the VPA biomass estimates to the values of the input quantities. Furthermore, the derivatives can be transformed into dimensionless sensitivity factors by scaling them:

$$(14)\quad S_{ik} = \frac{x_k}{B_i} \cdot \frac{\partial B_i}{\partial x_k}$$

where S_{ik} is our notation for the sensitivity in year i of the biomass estimate B_i to the input factor x_k. The interpretation of the S_{ik} is that for a given percentage change in the corresponding x_k, the biomass estimate will change by that percentage multiplied by S_{ik}. Such sensitivities are similar to the quantities defined by economists as *elasticities*. (Clark 1976, p. 128). Sensitivities were computed for all input factors except the weights at age.

Multiple Biomass Estimates for Each Year

We made several runs of our VPA algorithm with different assumptions about the variance in M. Also, runs were made to examine the effects of values of the FTC other than 1.0. Table 1 lists the various runs and their parameters.

Results

VPA and Variance Estimates

Figure 2a is a time-series plot of the VPA biomass estimates from run 22, with approximate 95% confidence intervals. The confidence bounds were calculated as the population estimate ±2 standard errors; the standard error is the square root of equation 6. The very large confidence intervals from 1929 to 1939 largely result from the poor precision of the estimated weights at age during these years. In later years, the CV of the estimates is much lower.

Figure 2b illustrates the CV's of the VPA biomass estimates from runs 20 and 21. (Since runs 20–22 vary only in their treatment of the variance of natural mortality, the biomass estimates are identical.) The CV's of run 20 are largest and those from run 21 smallest. Run 22 falls in between, but somewhat closer to run 20.

Composition of Variance

Figures 3a, 3b, and 3c show the time-averaged compositions of the variance estimates from runs 20, 21, and 22. In preparing this figure, we have omitted the highest variance years, 1929–39. In each case, the largest fraction of the mean variance comes from the estimates of M, for which we assumed a CV of approximately 25%. The other large fraction comes from the estimates of weights at age. Smaller fractions come from the catch at age, total catch, and the FTC. All other fractions of the variance were less than 0.05%. The results for runs 23 and 24 were essentially identical to those of run 22.

Effects of F Transfer Coefficient

We found that the variance of the FTC was relatively unimportant in establishing the total variance (Fig. 3), contributing at most 2.3% of the total in years after 1935. The mean value of F_4 for these years was 1.01. In earlier years, however, when the mean value of F_4 was only 0.16, the FTC contributed up to 12% of the total variance. Changing the value of the FTC had little effect on the biomass estimates except in the initial years with low F (Fig. 4). This small effect is in agreement with the low sensitivities to FTC (<1%) that we found when F was moderate or high.

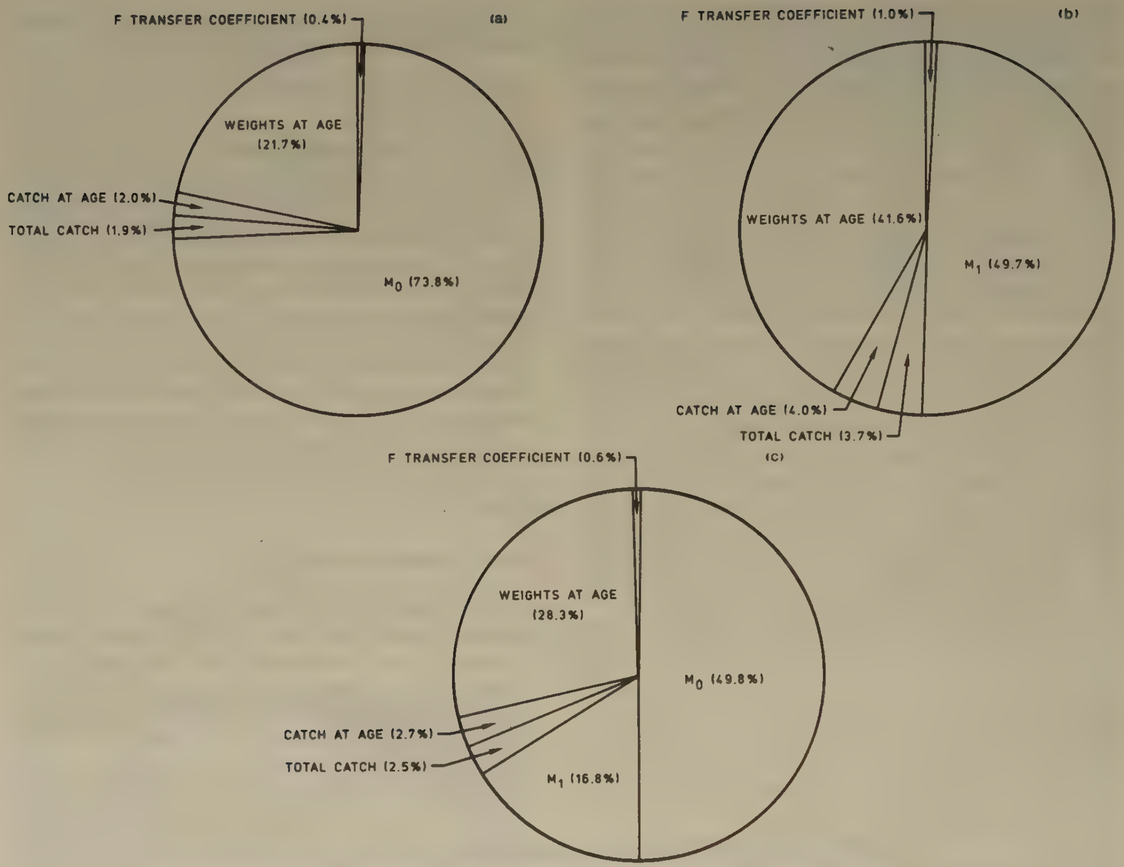

FIG. 3. Variance composition for runs 20, 21, and 22. Results of runs 23 and 24 are extremely similar to those of run 22.

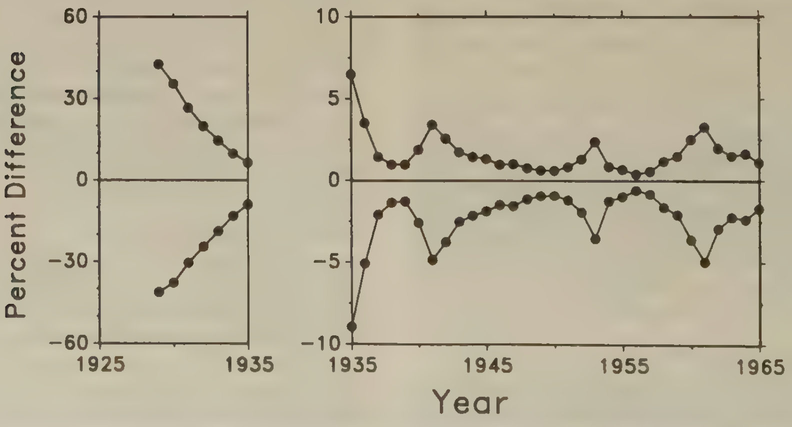

FIG. 4. Biomass estimates from runs 23 (lower curves) and 24 (upper curves), which have FTC values of 1.25 and 0.90, respectively. Plots are of percentage differences from run 22. To illustrate the different scales, the 1935 values are shown in both panels.

TABLE 2. Dimensionless sensitivities (S_{ik}, equation 14) of VPA biomass estimate in 1955 to various input quantities. Sensitivities are for run 22 and vary in other years and runs. Factors less than 0.01 are not shown.

Input quantity, x_k	Sensitivity of 1955 biomass estimate to this quantity
Low-frequency M (M_0)	0.359
High-frequency M (M_1) in 1955	0.178
M_1, 1956	0.109
M_1, 1957	0.045
M_1, 1958	0.016
Total catch, 1955	0.291
Total catch, 1956	0.332
Total catch, 1957	0.269
Total catch, 1958	0.079
Total catch, 1959	0.015
Total catch, 1960	0.010
Catch (1955, age 3)	0.033
Catch (1956, age 2)	0.056
Catch (1956, age 3)	0.128
Catch (1956, age 4)	0.047
Catch (1957, age 3)	0.060
Catch (1957, age 4)	0.070
Catch (1957, age 5)	0.060
Catch (1958, age 4)	0.032
Catch (1958, age 5)	0.037
Catch (1959, age 5)	0.024
Catch (1960, age 5)	0.012

TABLE 3. Dimensionless sensitivities (S_{ik}, equation 14) of VPA biomass estimates to various input quantities. Sensitivities are means for the years 1940–65; those less than 0.01 or related to catch at age are not shown.

Input quantity, x_k	Mean sensitivity of biomass estimates to this quantity
Low-frequency M (M_0)	0.360[a]
Low-frequency M (M_0)	0.821[b]
High-frequency M (M_1), year i[c]	0.176[a,d]
High-frequency M, year i + 1	0.108[a,d]
High-frequency M, year i + 2	0.062[a,d]
Total catch, year i	0.360
Total catch, year i + 1	0.272
Total catch, year i + 2	0.185

[a] Assumes that natural mortality and its variance are divided evenly between low-frequency (M_0) and high-frequency (M_1) components.

[b] Assumes that natural mortality and its variance are entirely in the low-frequency component (M_0).

[c] Year i is the year of the estimate.

[d] If natural mortality were entirely in the high-frequency component, this sensitivity would be approximately doubled.

Sensitivity Factors

Using equation 14, we computed sensitivities to each input quantity for each year's biomass estimate. Table 2 shows the sensitivities for run 22 in 1955, which is considered typical. Factors less than 0.01 are not shown.

For run 20, the sensitivity to M_0 is approximately doubled from Table 2. For run 21, the sensitivity to M_1 is approximately doubled from Table 2.

Table 3 shows mean sensitivities for the years 1940–65. Sensitivities to specific catches at age are omitted from the table; such sensitivities are in general small (<0.05) and vary from year to year. Of them, the greatest sensitivities are to catches at age 5, probably because these are the heaviest fish and because numbers at age 5 are magnified by the backwards VPA algorithm. Table 3 reveals that, as expected, VPA biomass esti-

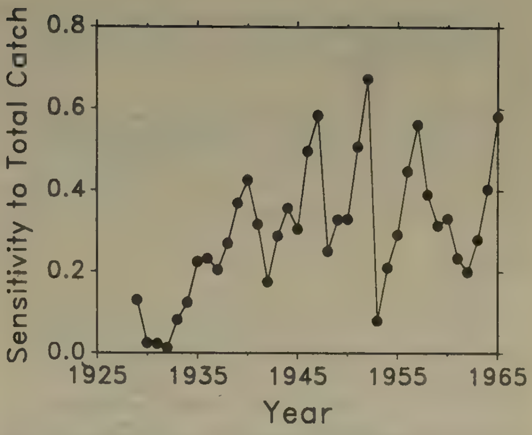

FIG. 5. Sensitivity of biomass estimates to total catch in the year of the estimate.

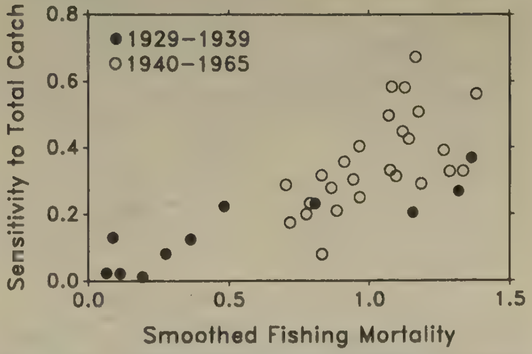

FIG. 6. Effect of fishing mortality (F) on the sensitivity of biomass estimates to total catch in the year of the estimate. The smoothed F values on the x-axis are arithmetic means of F in the year of the estimate and in the next three years.

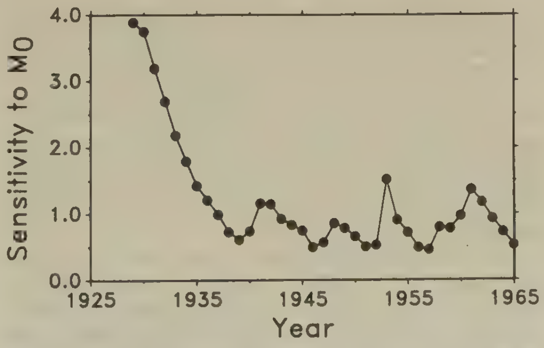

FIG. 7. Sensitivity of biomass estimates to low-frequency component of natural mortality (M_0). All natural mortality is assumed to be in M_0; if half were in the high-frequency component, sensitivities would be approximately halved.

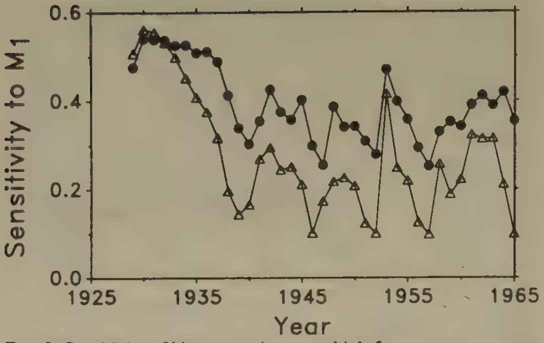

FIG. 8. Sensitivity of biomass estimates to high-frequency component of natural mortality (M_1). Upper curve: M_1 in the year of estimate; lower curve: M_1 in the following year. All natural mortality is assumed to be in M_1; if half were in the low-frequency component, sensitivities would be approximately halved.

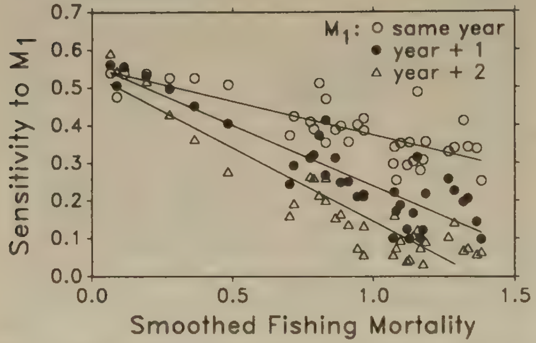

FIG. 9. Effect of fishing mortality (F) on the sensitivity of biomass estimates to the high-frequency component of natural mortality (M_1) in the year of estimate or in the following 2 yr. The smoothed F values on the x-axis are means of F in the year of the estimate and in the next 3 yr. Regression lines for each year are shown. As in Fig. 8, all natural mortality is assumed to be in M_1.

mates are highly sensitive to M; however, the highest sensitivity under the present assumptions was less than unity.

Figure 5 is a time plot of sensitivity to total catch in the year of the estimate. The sensitivity is less than 0.05 in 1930–32, when exploitation was very light, but rises to around 0.4 in later years. Figure 6 shows the same sensitivities plotted against smoothed estimated fishing mortality (F). The two tend to covary, even when the data are broken into pre-1940 and post-1939 groups. The years with highest estimated F were most sensitive to the value of catch.

Figures 7–9 describe the sensitivity of the biomass estimates to the estimate of M. Figure 7, a time plot of sensitivity to the low-frequency component (M_0) of natural mortality, demonstrates the very high sensitivities (nearly 4.0) in the years when the stock was lightly exploited. The sensitivities later fall to around 0.75. Figure 8 is a similar time plot of sensitivity to the high-frequency component (M_1) of natural mortality. The sensitivity is higher to M_1 in the same year as the estimate, but also significant to M_1 one year later. The shape of the two curves is nearly the same. Figure 9 demonstrates that, as expected, the sensitivity to M_1 depends on the intensity of exploitation. With higher values of F, the sensitivity to the value of M_1 decreases.

Discussion

We wished to estimate the variance of VPA biomass estimates so that the variances could be used in correcting a stock–recruitment model for the so-called "errors in variables" problem (Draper and Smith 1981). This problem, which arises when error is present in the predictor variable of a regression model, results in biased parameter estimates and can obscure stock–recruitment relationships (Walters and Ludwig 1981). However, knowing the variance of the biomass estimates is also valuable because it allows confidence bounds to be drawn about the population estimates (Fig. 2) and hypotheses about population sizes to be tested statistically. Since the composition of each variance estimate is also known (Fig. 3), the relative importance of better knowledge of each input quantity can be judged. This could prove useful in planning an efficient monitoring program for a stock.

Our variance estimates were slightly biased downward by the cohort analysis algorithm we used, which was selected to reflect the seasonal nature of the fishery (see Cohort Analysis above). In this algorithm, values of k (which depends upon M) were estimated separately and not changed when computing derivatives with respect to M. To have done otherwise would have been computationally impractical. However, a numerical investigation of the bias revealed it to be generally quite small. In the years after 1945, the bias was approximately 1 or 2% in the CV of biomass, i.e. a CV reported as 20% was probably about 21%.

The sensitivities we computed reveal the importance of errors in the inputs in an easily interpreted way. By using the sensitivities, one could estimate the probable error in the biomass estimate for a past year when M (for example) was thought to be unusually high or low. Also, such sensitivities can be used for an objective and uniform analysis of any model. Being dimensionless, they provide a scale-free expression of the relationship of a model to its input factors.

Omission of Recent Years from Calculations

In general, the variance in VPA estimates is highest for the most recent years, when cohorts have been fished for few years and the effect of error in the estimate of terminal F is not reduced by convergence. However, Fig. 2 shows no such effect. This is because we restricted our analyses to those years which permitted running the analysis with only one estimate of terminal F: the $F_5{}^+$ in 1969. Thus, although our data ran through 1969 (the final year of data available before the collapse of the stock), our "historical" estimates of population biomass and its variance run only through 1965. The variances of "current" VPA estimates (those nearer the final year of data) would of course be higher. Also, estimates of such variances would be much less precise; the variance of a "current" VPA estimate is almost entirely a function of the variances of M and the terminal F for the cohort, both typically quite high.

Further Applications of the Method

The delta method is a valuable tool for estimating the variances of complex models. We have applied it to VPA biomass estimates, but it could be used equally well on other quantities estimated by VPA. For example, the variances of full iterative VPA could be estimated, although the computations would be more lengthy. Also, the same methodology could be used to estimate the variances of fishing mortalities or population sizes in numbers arising from VPA. A further potential application wuld be the estimation of the variances of the parameters of "separable" VPA (Doubleday 1976; Deriso et al. 1985), in which the matrix of F's is estimated as a series of additive year and age effects. Finally, we expect that as fishery scientists become increasingly concerned with correcting for the effects of errors in variables, the delta method will prove an especially useful addition to the analytical toolbox.

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8854

CHANGING THE SIZE LIMIT: HOW IT COULD AFFECT CALIFORNIA HALIBUT FISHERIES

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ABSTRACT

The minimum legal size limit for California halibut (*Paralichthys californicus*) is 559 mm TL for all fisheries. There appears to be a conflict of allocation among user groups, with recreational catches being preempted by intense commercial fishing. We evaluate two possible solutions: a uniform change in the minimum size limit to 660 mm for all fisheries, or a differential size limit (recreational = 559 mm, commercial = 660 mm).

The commercial fishery takes from 60% to 80% females, which grow longer than males. Because sexes are not identified in most of the fishery data, we examined two alternative interpretations. In one case we treated the catch as consisting entirely of female fish; in the other case we treated catches as a combination of males and females, with a common, intermediate growth curve. We also examined two possible levels of natural mortality rate: $M = 0.1$ and $M = 0.2$. The virtual population analysis gave average total biomass estimates of 2,600 to 6,000 MT, and average recruitment (age 1) estimates of 0.5 to 1.0 million fish.

Yield-per-recruit (Y/R) analysis indicates that overall fishing effort is about twice the optimum level and that Y/R would likely increase with reduced fishing effort. Our analysis of proposed size limit assumed present levels of fishing effort. Under a differential size limit the recreational fishery shows an increased Y/R, both in weight and in numbers, whereas the commercial fisheries experience a net loss. Under a uniform 660-mm size limit for all fisheries, if $M = 0.1$, the Y/R for both recreational and commercial fisheries increases in weight but not in numbers. For a higher natural mortality rate ($M = 0.2$), the Y/R is reduced in the combined sex analysis, but the case of a female-based catch shows slight gain. The yield-per-recruit analysis suggests that the California halibut fishery is currently utilized at the point of maximum yield and that proposed changes in minimum size are not likely to resolve allocation conflicts among user groups.

RESUMEN

El tamaño mínimo legal para *Paralichthys californicus* en todas las pesquerías es de 559 mm LT. Parece haber un conflicto en cuanto a las cuotas de captura asignadas a ciertos grupos de usuarios, dado que una intensa pesca comercial se apropria de las capturas recreativas. Dos posibles soluciones son evaluadas: un cambio general del tamaño mínimo a 660 mm para todas las pesquerías o un límite diferencial (recreacional = 559 mm, comercial = 660 mm).

La pesquería comercial captura 60% a 80% de las hembras, las cuales alcanzan un mayor tamaño que los machos. Dado que no se indica el sexo en la mayoría de los informes pesqueros, examinamos dos explicaciones alternativas. En un caso, se consideró una captura compuesta exclusivamente por hembras; en el otro, se consideraron capturas compuestas por machos y hembras, con una curva de crecimiento común e intermedia. Se examinaron además dos niveles de tasa de mortalidad natural: $M = 0.1$ y $M = 0.2$. El análisis de poblaciones virtuales dió estimaciones de la biomasa total promedio de 2.600 a 6.000 TM y del reclutamients promedio (edad 1) de 0.5 a 1 millón de individuos.

El análisis de la producción por recluta (Y/R) indicó que el esfuerzo pesquero general es aproximadamente el doble del nivel óptimo y que Y/R probablemente aumentaría con una reducción del esfuerzo pesquero. Nuestro análisis de los cambios propuestos en tamaño mínimo supone niveles de esfuerzo pesquero similares a los actuales. Si se adopta un tamaño mínimo diferencial, la pesquería recreacional muestra un aumento en Y/R tanto en peso como en número de individuos mientras que la pesquería comercial experimenta una pérdida neta. Bajo el criterio de tamaño uniforme de 660 mm en todas las pesquerías, con $M = 0.1$, el Y/R de ambas pesquerías aumenta en peso pero no en número de individuos. Con una mortalidad natural más alta ($M = 0.2$), el Y/R es menor en el caso de un análisis con sexos combinados, pero en el caso de una captura compuesta sólo por hembras muestra un leve aumento. El análisis de producción por recluta sugiere que, actualmente, la pesquería de

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[Manuscript received February 19, 1988.]

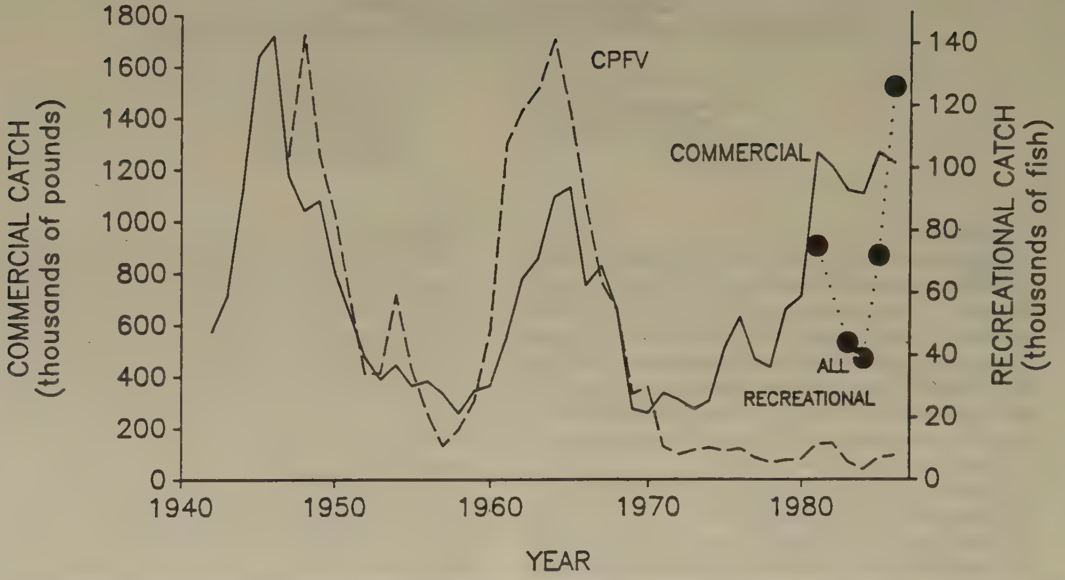

Figure 1. History of California halibut catch, 1947–85. Commercial landings (*solid line*) are reported in pounds. Commercial passenger fishing vessel (CPFV) landings (*broken line*) and total estimated recreational catch (Anon. 1984–87; *dotted line*) are reported in numbers of fish.

P. californicus en California es utilizada a un nivel de producción máximo y que los cambios en tamaño mínimo propuestos probablemente no resolverían los conflictos en cuanto a las cuotas asignadas a los grupos de usarios implicados.

INTRODUCTION

California halibut (*Paralichthys californicus*) is an important food and game fish, utilized heavily by both commercial and recreational fishermen in central and southern California. To prevent overexploitation of the resource, a uniform legal minimum size limit of 22 in. (559 mm) TL was enacted in 1971, with an allowance for a small number of undersized fish for the commercial fisheries. The expected result of this regulation was an initial decrease in the catch with an eventual recovery over the time period required for the halibut to grow to the minimum legal size and for the population to experience recruitment from a larger spawning population. Following this legislation, the recreational commercial passenger fishing vessel (CPFV) catch dropped from 29,451 fish in 1970 to 10,435 fish in 1971 and has continued at this low level, while commercial landings have increased in a pattern typical of historical catches, from 272,000 pounds in 1971 to 1,260,000 pounds in 1985 (Figure 1).

The recreational catch of California halibut includes the catch from four general fishing modes: CPFVs, man-made structures, private boats, and shorelines. Although CPFV catches have been reported annually since 1947, data on all recreational fishing modes are available for only two relatively short periods. These studies indicate that the contribution of CPFV-caught fish to the total recreational halibut catch has decreased from approximately 40% in the mid-1960s (Pinkas et al. 1968) to about 10% in 1981–84 (Anon. 1984, 1985). Thus the recreational halibut catch may have recovered more than the CPFV catch indicates (Figure 1), but not to catch levels previously experienced.

Methot (1983) described the status of the California halibut resource as "uncertain." However, halibut length frequencies observed in commercial fish-market samples are relatively stable, and both the recreational and commercial fisheries have persisted through what appear to be cyclic decreases in the halibut population. Therefore we assume that the fisheries are at approximate equilibrium. But there is a conflict among user groups, with recreational catches appearing to be preempted by intense commercial fishing. Accordingly, the primary management problem is a matter of allocating the catch among the user groups. A management strategy that would improve recreational catches without seriously impacting the commercial yield would reduce the conflict between recreational and commercial users. In this paper we examine increasing the size limit to achieve such a strategy.

Two management alternatives to improve allocation of the California halibut resource are being considered by the California Department of Fish and Game: (1) a uniform size limit of 660 mm (26 in.) to allow the halibut an additional reproductive season before recruitment, or (2) a differential size limit (recreational = 559 mm or 22 in; commercial = 660 mm or 26 in.) to make more legal fish available to recreational anglers. The California halibut catch is presently regulated via a minimum size limit and some commercial gear limitations. The proposed changes in size limit are in keeping with current management strategies for this species, and we presume they could be implemented effectively. To evaluate the effect of these alternatives, we performed a yield-per-recruit analysis for multiple-gear fisheries using the program MGEAR (Lenarz et al. 1974) and data from records of the California Department of Fish and Game.

METHODS

Data

Three different general gear types are used to catch California halibut: (1) recreational hook and line; (2) commercial mobile gear (trawl, purse seine, lampara); and (3) commercial stationary gear (set net, entangling net, longline). The distinctions are made to identify user groups and to partition the fishing mortality rates among fishery segments.

Female California halibut grow faster and thus attain larger sizes at age than males. However, commercial and recreational landings have not been reported by sex categories, and until recently, the length-frequency information from fishery monitoring also has been for combined sexes. The sex of fish sampled from commercial catches was collected opportunistically beginning in late 1985. Females appear to represent 60% to 80% of the commercial landings (Calif. Dept. of Fish and Game, unpubl. data, J. Sunada, Long Beach), but these data contain biases resulting from fish-market cleaning and sampling practices.

Because true sex composition is unknown, we examined two alternative interpretations that include the true sex composition as an intermediate case: Schott[1] compiled a length-age key for combined sexes that included approximately 53% females, 26% males, and 21% unknown sex, as well as keys for individual sexes. This allowed us to base our analysis on Schott's "combined-sex" key as one extreme, and to treat the catch as being entirely female as the other extreme. To estimate population biomass in the latter case, we assumed landings of female fish to be 70% of the total landings.

Because data on female halibut exist only for the most recent years, data used in these two analyses are from somewhat different sources. Length frequencies from the recreational catch were sampled from 1981 through 1984 ($N = 396$; MRFSS 1981–84), but sexes were not identified (Figure 2). Length frequencies for commercial mobile gear were obtained from market samples of trawl-caught halibut; sampling was conducted from 1983 through 1986 ($N = 2{,}072$), but females were identified only in 1986 ($N = 124$). Length frequencies for commercial stationary gear were obtained from direct on-board observations of halibut caught by gill nets; these observations include undersized fish that are legally removed from the population (for personal use, etc.) but are not marketed. Length frequencies of halibut caught by gill nets were taken from 1983 to 1987 ($N = 4{,}219$), but females were identified only in 1986 and 1987 ($N = 695$).

The length-frequency information described above was used for two purposes: to convert the commercial catch, which is recorded in weight, to catch in numbers, and to estimate catch by age. We calculated the average weight of the fish in the length-frequency distributions by means of a length-weight relationship developed by Schott (Table 1). For each commercial fishery segment, we divided the average annual catch in weight (1981–86) by the corresponding estimated average fish weight to produce estimates of each segment's catch in numbers (Table 2). Recreational catches are reported in numbers (Anon. 1984–87). We then used the appropriate length-age key[2] to convert each length frequency to an age frequency, and multiplied by the estimated total catch in numbers to obtain the catches at age for use in the virtual population analysis.

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[1] Schott, J. W. Age and growth of California halibut *Paralichthys californicus* (Ayres). (Unpublished manuscript, California Department of Fish and Game files; available upon request from R. J. Reed.)

[2] Ibid.

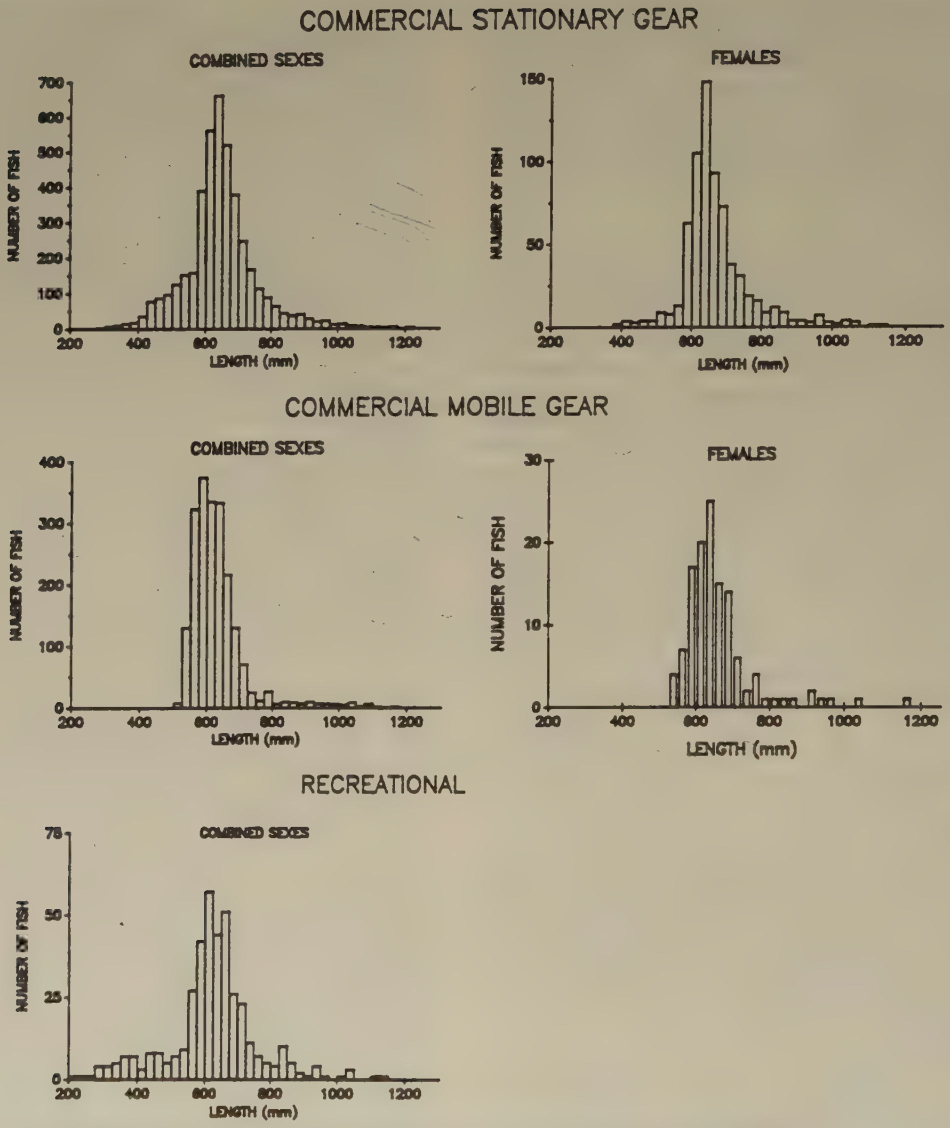

Figure 2. California halibut catch-length frequencies for major fishery segments and sex composition. Note: vertical scales differ.

Virtual Population Analysis

Age-specific fishing mortality rates were derived using virtual population analysis (VPA). In addition to the catches at age, VPA requires estimates of natural mortality and terminal fishing mortality rates. Estimates of the instantaneous natural mortality rate (M) ranged from 0.3, on the basis of related flatfish species at similar temperatures (Pauly 1979), to 0.15, on the basis of longevity (Hoenig 1983). We derived the latter estimate from the maximum known age of 30 years, which was obtained from sampling in the mid-1960s[3]. The es-

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[3] Ibid.

TABLE 1
Parameter Values of the von Bertalanffy Growth Equation and Length-Weight Regression for California Halibut

	Growth parameters			Length (mm)-weight (kg) parameters	
	L_{infinity}	k	t_0	a	b
Females and immatures	1417.42	0.1194	0.3801	0.000007768	3.0496
Males and immatures	1137.43	0.1218	0.1004	0.000009216	3.0165
Sexes combined	1217.51	0.1414	0.4073	0.000008807	3.0300

Adapted from Schott, J. W. Age and growth of California halibut *Paralichthys californicus* (Ayres). (Unpublished manuscript, California Department of Fish and Game files; available on request from R. J. Reed.)

timate using Hoenig's method reflects the total mortality rate, and because halibut have been exploited since the early 1900s, M would be expected to be lower than 0.15. In view of the longevity of California halibut, M could not possibly be as high as 0.3. We considered two arbitrary estimates of M (0.1 and 0.2) in order to explore the sensitivity of the yield-per-recruit analysis to a range of probable values of the natural mortality rate.

Our VPA employed a method described by MacCall (1986), which accounts for the seasonal pattern of catches by each segment of the fishery. In the present case, we used the equation:

$$N(t) = N(t+1)\exp(-M) + V_{\text{rec}}C_{\text{rec}}(t) + V_{\text{stat}}C_{\text{stat}}(t) + V_{\text{mob}}C_{\text{mob}}(t)$$

where $N(t)$ is abundance in numbers at the beginning of year t, $C(t)$ is catch in numbers during year t, and V is a coefficient that depends on the seasonal pattern of catches of the respective segment of the fishery (rec = recreational, stat = stationary commercial, mob = mobile commercial). Values of V were based on monthly catches by gill net and trawl gears from 1981 through 1986 (Calif. Dept. of Fish and Game catch records), and on bimonthly catches by the recreational fishery from 1984 through 1986 (MRFSS 1984–86). We calculated coefficients V for each year, and then averaged over the yearly values for each gear separately (Table 3).

TABLE 2
Average Annual Recreational (1980–84) and Commercial (1981–86) Catch of California Halibut

Fishery segment	Average annual catch		Average weight per fish (kg)
	Numbers	Weight (kg)	
Recreational	71,200 (15,695)	184,009 (40,016)	2.5844 (0.1040)
Commercial			
Stationary gear	141,066 (7,185)	426,330 (21,715)	3.0222 (0.0359)
Mobile gear	52,201 (7,449)	118,423 (16,900)	2.2686 (0.0438)
Total	264,467	728,762	

Standard errors are in parentheses.

We applied the VPA to the estimated age composition of the catch as a "synthetic cohort," which uses the average age composition of the catch over a relatively short period (3 to 6 years in this case) to approximate the age composition of a cohort over its lifetime. Lacking objective criteria, we calculated terminal fishing mortality rates (F) on the basis of internal consistency. We chose a terminal value (for ages 19 and older) of F that was equal to the average value of F for ages 11 through 18, given that terminal value. This approach gave a unique solution in each case, and depends only on the assumption that F is constant for ages 11 and older. Although we believe that this assumption is reasonable, we lack information by which to test its validity.

Yield per Recruit

Yield-per-recruit analysis requires growth information in addition to the mortality information derived above. Males and females grow at different rates, but, as noted earlier, sex composition of the catch is unknown. For the analysis based on an assumed all-female catch, we used the von Bertalanffy growth curve and length-weight relationship developed by Schott for female halibut. For the combined-sexes analysis, we used Schott's relationships for combined sexes (Table 1).

We modeled yield per recruit using the program MGEAR, which takes into account differences in

TABLE 3
Average VPA Coefficients That Compensate for Seasonality of California Halibut Fishery

	V_{rec}	V_{stat}	V_{mob}
Combined sexes			
M = 0.1	1.055437	1.047947	1.048698
0.2	1.114594	1.098704	1.100948
Females only			
M = 0.1	1.055437	1.047947	1.048698
0.2	1.114594	1.098704	1.100948

and interactions among fishery segments. Classical yield-per-recruit models have assumed instantaneous, or knife-edged, recruitment to the fishery at a given age. However, recruitment of California halibut occurs over a range of ages because of an allowance for the commercial take of undersized fish and because of differences in gear selectivity among the fishery segments. The program MGEAR allows for fish being recruited gradually and at different ages for different fishery segments by using age-specific *F* values for each fishery segment.

We estimated the effect of a change in size limit by using a modified set of age-specific *F* values. Selectivity curves for the various gears are not known, requiring an indirect method: for each gear, we assumed the peak value of *F* to indicate the age of full availability, and calculated availabilities of younger ages relative to that value. For each of the younger ages, we then used the information in Schott's length-age keys to estimate the length percentile corresponding to the retention rate implied by the availability as if retention were knife-edged.

For example, if availability was 0.8, we calculated the "selection length" at which 80% of the fish were larger. We then assumed that the unknown mechanisms leading to that selection length would change in proportion to the proposed change in size limit, which in the present case is 660 mm/559 mm, or an increase of 18%. Accordingly, we then determined the length percentile corresponding to an 18% increase in the selection length. We assumed that this new percentile represents the modified availability under the new size limit. We multiplied the estimate of modified availability by the peak *F* that was assumed to represent full availability, thereby obtaining the modified set of age-specific *F* values for use in the yield-per-recruit analysis (Figure 3). To measure the effect of the uniform and differential size-limit policies, we compare the yield per recruit (Y/R), in weight and in numbers of fish caught, to the Y/R under the current uniform 559-mm size limit to determine the relative percentage change.

RESULTS AND DISCUSSION

Estimates of Abundance

Although our VPA estimates were based on "synthetic" rather than actual cohorts, the results provide estimates of the approximate magnitude of the California halibut resource. The estimates vary with the assumed rate of natural mortality and with the treatment of the sex composition of the catches (Table 4). The probable total biomass is estimated in the range of 2,600 to 6,000 MT. Abundance estimates based on all-female catches must be augmented by a presumed biomass of males, which is somewhat smaller because of their smaller weights at age, but would fall within the above range. Recruitment, in number of fish at age 1, may be treated similarly; estimates based on female catches, which we have assumed to be 70% of the total, should be increased about 30% to include males. Thus we estimate annual recruitment to be between 0.45 and 1.0 million fish (Table 4). The estimates provided by "synthetic" cohorts are, in a poorly defined way, average values. If the record of catches (Figure 1) is any indication, actual

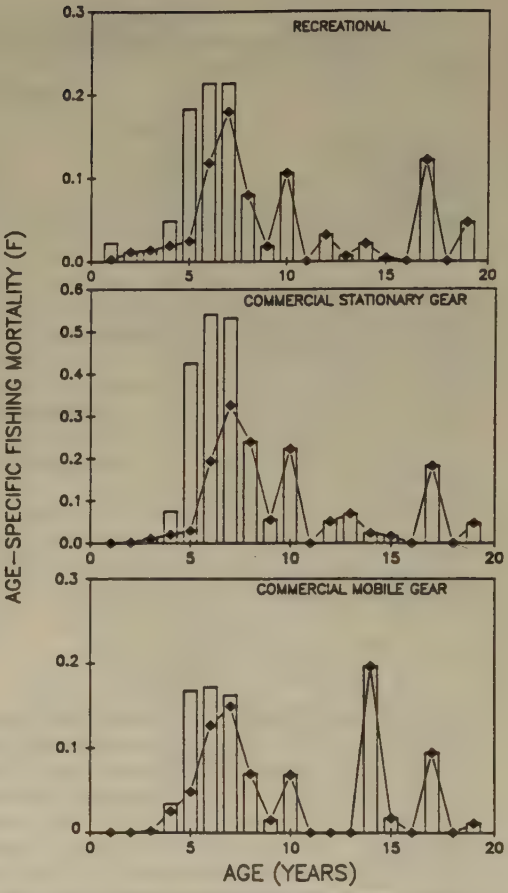

Figure 3. An example of the change in age-specific fishing mortality (*F*) to simulate the increase of the minimum California halibut size limit from 559 mm to 660 mm. Treatment is all-female catch, $M = 0.1$.

TABLE 4
VPA Estimates of Biomass and Recruitment of California Halibut

Assumed natural mortality rate	Treatment of catches	
	Combined sexes	Females only
$M = 0.1$	$B = 2{,}600$ $R = 450{,}000$	$B = 2{,}300$ $R = 430{,}000$
$M = 0.2$	$B = 6{,}000$ $R = 950{,}000$	$B = 3{,}200$ $R = 750{,}000$

Biomass (B) in metric tons; recruitment at age 1 (R) in number of fish.

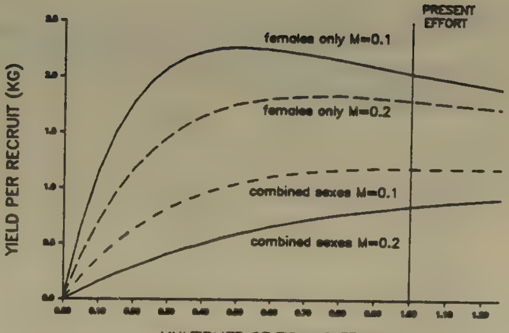

Figure 4. Yield per recruit for California halibut at different levels of fishing effort. Present level = 1.0.

biomasses may have varied as much as fivefold, and recruitments have varied much more.

Present Status of the Fishery

Before examining the individual segments of the fishery, it is useful to evaluate the status of the fishery as a whole, particularly with regard to the overall level of fishing intensity. Given the present patterns of size selectivity or age selectivity, and relative intensities of the three fishery segments, the resource is probably overfished (Figure 4); i.e., a reduction in fishing intensity would increase total catch in biomass. Both of the cases where M was assumed to be 0.1 show peak Y/R at fishing intensities lower than present levels. In the cases where M is assumed to be 0.2, the present fishing intensity is at peak Y/R for the all-female case; only for the combined-sexes case is peak Y/R to be found at fishing intensities higher than the present level.

Optimal levels of fishing intensity are nearly always below those that produce maximum yield per recruit. One popular rule of thumb is the $F_{0.1}$ policy suggested by Gulland and Boerema (1973). This policy establishes a nominal upper limit to fishing intensity as the level at which the marginal increment in catch per effort is one-tenth that of a nearly unfished resource. In three out of the four cases shown in Figure 4, the $F_{0.1}$ policy indicates optimal fishing intensities in the vicinity of one-half the present level. Only in the case of $M = 0.2$ and combined-sex treatment of catches is the $F_{0.1}$ level of fishing intensity above the present level. It is our opinion that the latter case is the least likely of the four cases examined, because M is probably much lower than 0.2, and the catch is known to consist mostly of female fish.

Changes in Yield per Recruit

Under a uniform 660-mm size limit for $M = 0.1$, the Y/R increased for all fishery segments, by weight but not by number (Table 5); larger but fewer halibut were caught. When $M = 0.2$, the Y/R shows a loss for all fishery segments in weight and number assuming combined sexes, and no significant gain assuming a fishery based solely on female fish. It would appear that some benefit would be realized under a uniform 660-mm size limit, given the lower natural mortality rate. However, the commercial catch is valued by weight (pounds of fish sold), whereas recreational anglers tend to value their catch based on the number of fish caught (Fritz and Schuler 1984). Therefore we assume that a strategy which reduces the number of fish in the recreational catch would not alleviate the current allocation conflict.

Under a differential size limit, the recreational Y/R increases by weight and by number in all cases (Table 5), but the commercial stationary gear Y/R shows a concomitant decrease. The Y/R for commercial mobile gear increases for a catch based on female fish but tends to decrease for a catch based on both sexes. A differential size limit will improve the recreational fishery segment, but at the expense of commercial fishery segments.

Since females grow faster than males, an increased minimum size limit is expected to increase the percentage of females in the catch. Recent data indicate that the commercial catch is already biased toward females. Of the four cases examined, the least benefit would be expected when the natural mortality is high and males are included in the catch with females. The net change in Y/R for the entire fishery suggests that some benefit would be realized with an increase in size limit, except in the last case.

This analysis simulates an increase in size limit by decreasing the availability of smaller fish, and does not consider the possibility of a concomitant increase in availability of larger fish. Because the

TABLE 5
Percentage Change in Yield per Recruit by Weight and Number ( ) under a Differential Size Limit (559-mm recreational/660-mm commercial) and under a 660-mm Uniform Size Limit Compared to a Uniform 559-mm Size Limit

Male and female combined catch	Recreational	Commercial		Entire
		Stationary gear	Mobile gear	
M = 0.1				
Uniform	+17 (−23)	+8 (−30)	+37 (−2)	+16
Differential	+85 (+54)	−21 (−45)	+3 (−22)	+18
M = 0.2				
Uniform	−9 (−29)	−15 (−35)	−53 (−72)	−21
Differential	+41 (+29)	−24 (−41)	−59 (−75)	−28
Female catch only				
M = 0.1				
Uniform	+38 (−11)	+12 (−31)	+69 (+15)	+31
Differential	+90 (+54)	−14 (−45)	+31 (−6)	+21
M = 0.2				
Uniform	+14 (−16)	−12 (−41)	+29 (−4)	+3
Differential	+59 (+37)	−25 (−49)	+13 (−14)	+3

commercial net gears used to catch California halibut tend to be size selective, a possible means of implementing a differential size limit would be via an increase in minimum mesh size. It is possible that, due to differences in mesh selectivity, catch rates of older fish might increase (Hamley 1975). Preliminary comparisons of the performance of commercial halibut gill nets of different mesh sizes indicate an increase in the availability of larger fish (Calif. Dept. of Fish and Game, unpubl. data, K. Miller, Long Beach). This is a case we were unable to analyze with available data. However, any increase in the catch of older fish could compensate for the loss of smaller fish resulting from an increase in the size limit. This would increase the relative percentage change in Y/R for the affected fishery segment. A change in the selectivity of commercial stationary gear or similar increase in the availability of larger fish could change our conclusions regarding the utility of a change in size limit.

CONCLUSIONS

Although Y/R increased by weight under a uniform 660-mm size limit, we assume that this management strategy would increase recreational users' dissatisfaction by decreasing the number of fish in the catch. Alternatively, the differential size limit would be expected to increase recreational satisfaction by increasing the number of fish in the catch. Unfortunately, this increase would substantially impact the commercial fishery segments, particularly commercial stationary gear, which represents over 67% of all commercial landings. The results of this yield-per-recruit analysis indicate that allocation conflicts among user groups are not likely to be resolved by a management strategy that increases the minimum size limit. Instead, the fishery is most likely to benefit from a management strategy that limits fishing effort to $F_{0.1}$ or similar optimum yield level.

ACKNOWLEDGMENTS

We are grateful to Jack Schott, whose work provided information essential to this analysis. Other data for the analysis was willingly provided by Steve Crooke, Christine Pattison, John Sunada, and Marija Vojkovich. We also appreciate the comments received from Harold Clemens, Robson Collins, and two anonymous referees who critically reviewed this manuscript. This work was partially funded as part of Dingell Johnson project F-32-R, "Southern California Sportfish Research Program," supported by Federal Aid to Fish Restoration Funds.

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Appendix 2

THE RELATIONSHIPS BETWEEN LENGTHS OF CAPTURED BOWHEAD WHALES, YEAR OF CAPTURE AND VILLAGE

S. Reilly and M. Nerini

Results presented in SC/39/PS22 indicated there had been a significant increase in the annual average length of landed bowhead whales over the period 1973–87. Two issues were raised in the sub-committee regarding these results. First it was suggested that the increase was due primarily to captures made by a single village (Wainwright): verification of this suggestion was requested. Second, the sub-committee questioned whether the trend had continued beyond the 1981 recommendation that the catch select for smaller whales. This Appendix provides information on these two matters.

Rather than analysing annual mean lengths, this analysis was carried out using lengths recorded from the 216 whales landed during the period 1973–86. To test for the influence of Wainwright we regressed length on both year and village, with two groups defined: Wainwright and "Others". Overall, there was a significant increase in the length of landed whales ($p = 0.002$). The regression coefficient for village was large (4.4, $P(t) < 0.001$). The coefficient for year was small, but still significantly different from zero (0.13, $P(t) < 0.01$).

Lastly, repeating the regression of annual means weighted by the inverse of the variances (as in SC/39/PS22) but using 1981–6 data only, there is no significant trend in length of landed whales ($P = 0.45$). We conclude from these findings that the increase over the entire time period was due predominantly to Wainwright landings. Also, even for this village, there has been no trend in length of landed bowheads since 1981.

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Indices for Mid-Latitude North Pacific Winter Wind Systems; an Exploratory Investigation

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ABSTRACT: Biological distributions and fish migrations during the spring and summer in the mid-latitude N Pacific are believed to be affected by the large-scale wind systems during the preceding winter. These wind systems are related to the field of atmospheric pressure which, on a monthly or quarterly time scale, show pronounced interannual variations. This exploratory investigation is concerned with measures of the large-scale wind systems that are indicative of their intensity, location, and size, and that can be derived from monthly or quarterly sea-level pressure distributions. Of interest are the NW, W, and SW wind systems which are related to the pressure gradients between the Siberian High and Aleutian Low, the Aleutian Low and the N Pacific Subtropical High, and the Aleutian Low and the N American High, respectively. Interannual changes in the winter sea-level pressure distribution pattern are primarily the result of changes in the pressure and zonal displacements of the Aleutian Low near 50°N. This property permitted simple derivation of wind indices from grid values of N hemisphere mean winter pressures distributions for the years 1947 to 1985. Indices, presented as normalized anomalies, are for the meridional component of the wind system at 50°N over the ocean W and E of the Aleutian Low, for the westerlies S of the Aleutian Low and for the longitude of this Low. The paper concludes with a discussion of the limitations of the indices in terms of reflecting characteristic atmospheric pressure distribution patterns, an examination of the relationship between wind anomalies and El Nino events, and a discussion of the results in terms of oceanographic, climate, and biological implications.

Introduction

The wind stress at the sea surface is the key factor in the transfer of heat, moisture, and momentum between ocean and atmosphere. These processes affect not only the ocean-atmosphere climate system but also properties of water motion. Water motion such as is involved in mixing of the surface layer and wind driven surface currents are believed to affect biological processes, particularly those involved during the early stages of life. Currents, either directly or indirectly, may also affect the distribution and migration of marine life. It is useful, therefore, to investigate whether monthly or quarterly measures of the wind systems over the mid-latitudes of the N Pacific can be developed that are indicative of their intensity, location, and size.

In this exploratory investigation it is simpler and more instructive to infer properties of the wind systems from sea level atmospheric pressure distributions than from averages of directly observed winds as often is done in climatological investigations. Eber and Sette (1959) calculated indices of the mean monthly geostrophic wind over the N Pacific for the years 1926 to 1958. The indices were pressure differences determined at 36 locations over the principal currents from pairs of sea level pressures 350 to 600 nautical miles apart. In the present investigation interest is in indices of the large-scale wind systems derived from the major pressure systems rather than in geostrophic winds over limited sections of the ocean. This approach, however, can be used only during mid-summer and mid-winter when the pressure systems are well developed.

Air-sea interaction processes over the mid-latitude N Pacific are most active during the fall and winter months. It is believed that during these months oceanographic conditions are created that will persist and affect biological distributions and fish migrations during the subsequent spring and summer. This investigation, therefore, is concerned only with indices that reflect anomalies in winter wind systems rather than with those, such as the Eber-Sette indices, that can be used in time-series analyses.

North Pacific Mid-Latitude Winter Wind Systems

The long term mean January sea level pressure chart reproduced from Fleet Numerical Oceanography Center (FNOC) files (Fig 1) shows that the Aleutian Low (AL) dominates the mid-latitude N Pacific. The lowest pressure occurs near latitude 50°N and longitude 175°E. A ridge of high pressure extends across the Pacific from America to Asia between latitudes 20° and 30°N, with the highest pressure occurring near latitude 30°N and longitude 130°W. This cell of highest pressure is referred to as the Subtropical High (STH) and is linked to the Continental High over W N America. On the W side of the N Pacific the pressure of the ridge increases and is linked to the Siberian High (SH) near latitude 48°N and longitude 95°E. (The SH is outside of the area shown in Fig 1 but near the same position in Fig 2). In contrast to the winter pattern when the AL dominates, in summer the Subtropical High dominates over the N Pacific (Fig 1, lower panel).

Associated with these pressure cells are the principal wind systems. The dominant system in

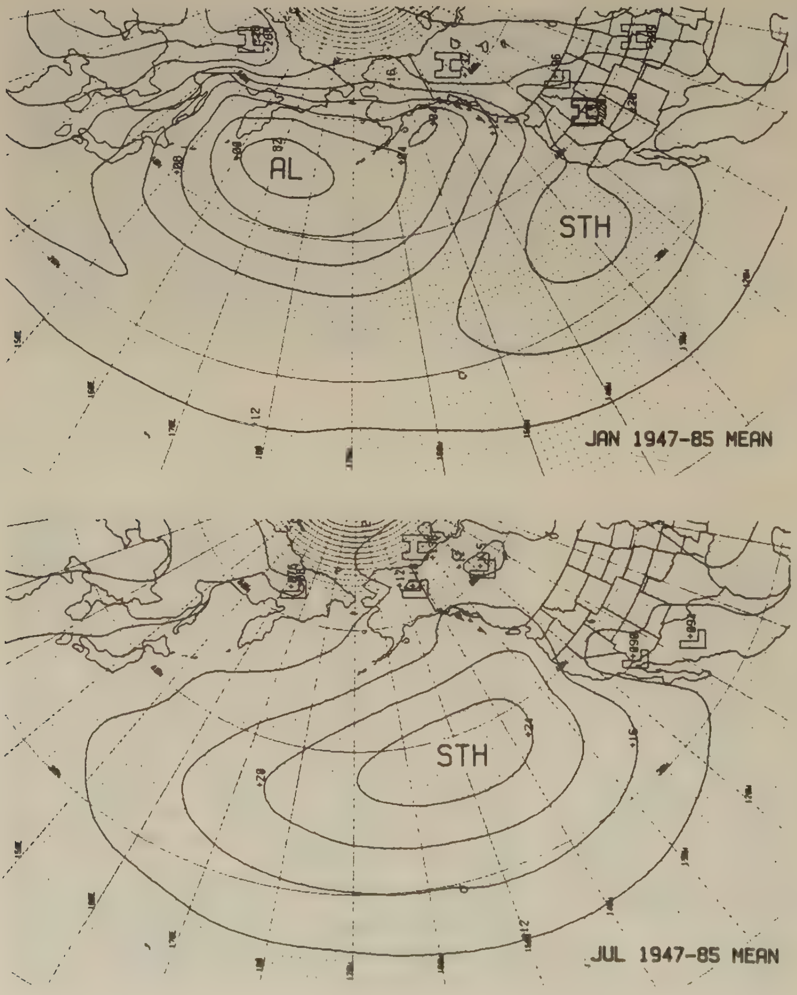


Fig 1
Sea level pressure, 1947-85 mean January, upper panel; 1947-85 mean July, lower panel

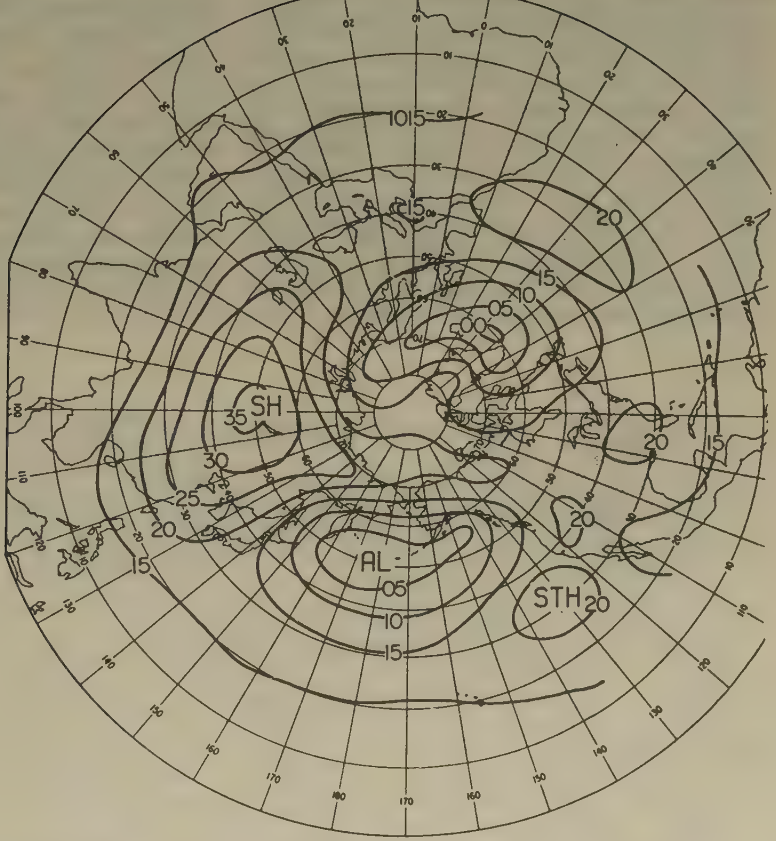


Fig 2
Winter sea level pressure, 1947-72 mean (Namias 1975)

winter, the westerlies, is that produced by the pressure gradient between the AL and the ridge of high pressure to the S (Fig 1). Another winter wind system is that produced by the pressure gradient between the AL and SH pumping cold, dry Arctic air over the W N Pacific. On the E side of the ocean the pressure gradient between the AL and the high pressure over N America produces a southerly wind component with warm, humid air. An all year system that is not a part of this investigation, the NE trades, is produced by the pressure gradient between the subtropical ridge of high pressure and the equatorial pressure trough. The cyclonic circulation about the AL, therefore, consists of three wind systems: The northwesterlies over the W, the westerlies over the central, and the southwesterlies over the E N Pacific. Because the December and February sea level pressure patterns resemble the extremum pattern in January the mean winter (December, January, and February) sea-level pressure distribution is similar to the January pattern (Fig 2).

From the sea-level pressure pattern shown in the lower panel of Fig 1 it is evident that the trade wind system is the dominant N Pacific wind system during the summer. On the W side of the ocean winds have a weak southerly component but on the E side the high gradient between the STH and the low pressure over California produces strong winds with a northerly component. The seasonally altering wind directions produce upwelling in summer and downwelling in winter along the mid-latitude coast of North America (Bakun 1973; Nelson 1977).

Individual Year Sea Level Pressure Distributions

The January sea level pressure patterns and their associated wind systems, vary from year to year and distinct types of distributions can be recognized. The examples shown are reproduced from FNOC files. The first pair of pressure patterns with a well developed AL (Fig 3) illustrate differences in the STH. In 1955 (upper panel) the STH is a separate, identifiable pressure system but in 1961 (lower panel) the STH appears only as a projection of the North American High extending out over the E Pacific. The STH is therefore not always a distinct pressure cell as it appears in long-term mean pressure charts. Other types of distribution patterns are primarily related to changes in size and location of the AL. Examples are shown in Fig 4 where the AL was displaced from its central Pacific location eastward into the Gulf of Alaska as in 1958 (upper panel) or westward toward Kamchatka as in 1969 (lower panel). Fig 5 shows an example of a ridge of high pressure (a blocking ridge) splitting the AL into an E and W cell as in 1956 (upper panel), and an other example, as in 1971 (lower panel), when the AL is not well defined. During some winters the E mid-latitude N Pacific is dominated by high pressure. In this distribution the pressure gradient E of the AL, but not necessarily the position of the AL, is displaced westward. Fig 6 shows an example that occurred in 1957.

From these subjective descriptions of pronounced differences in the pressure distribution patterns one can infer that there must be pronounced year to year variations in the intensity, location, and size of the principal wind systems. The question to be addressed below then is: can simple indices be derived that reflect the dif-

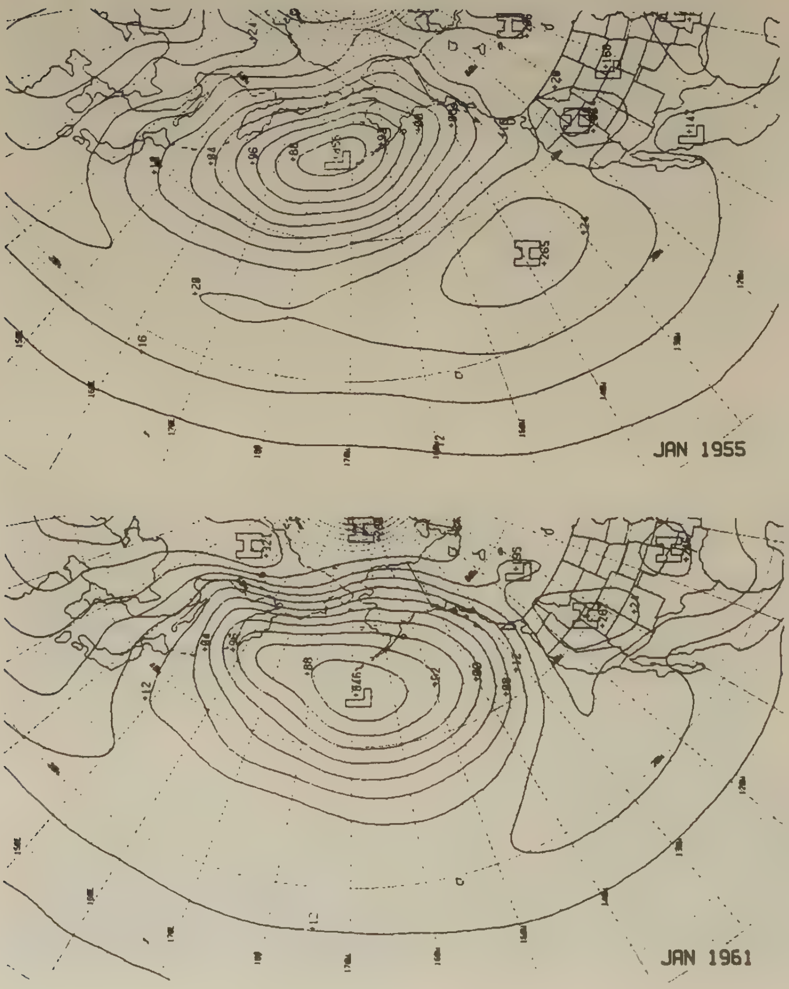


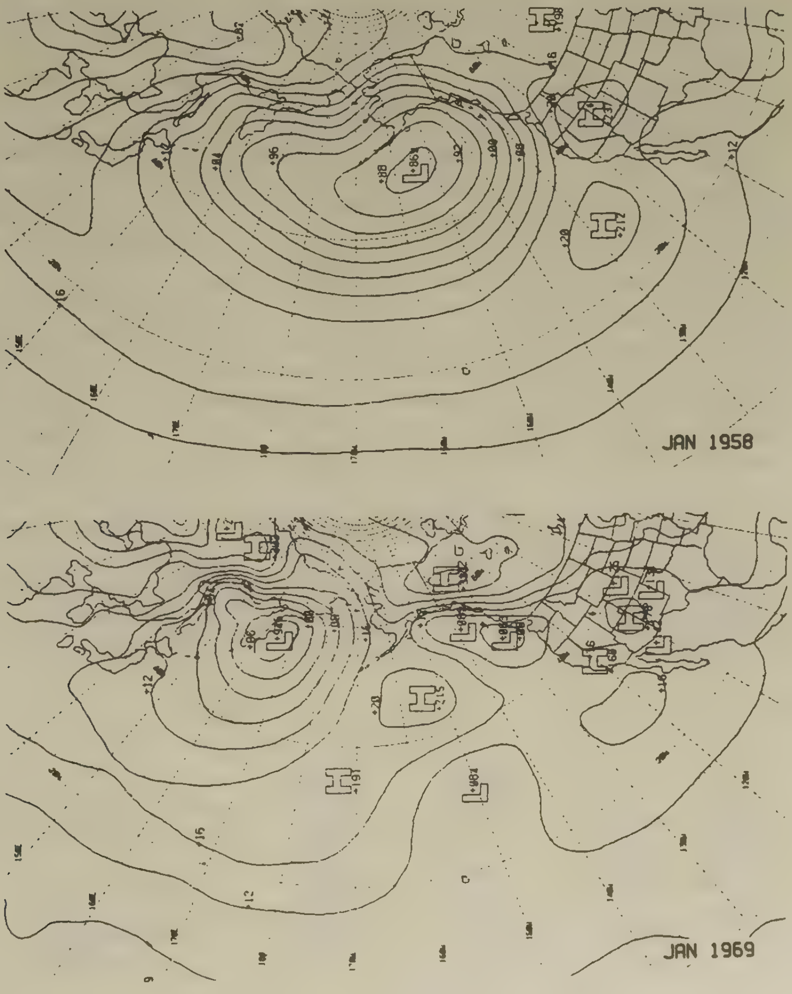
Fig 3
Sea level pressure, January 1955, upper panel; 1961, lower panel

ferences in the atmospheric pressure patterns as well as the characteristics of the associated wind systems?

Location of Atmospheric Pressure Centers

To begin the investigation, the 1951 to 1983, monthly mean January sea level atmospheric pressure charts produced by the National Meteorological Center, were used to pick the latitude and longitude of the AL, SH, and STH. The positions are approximate because (1) the charts ranged from the initial hand-contoured to the present computer produced versions with methods of production changing with advancing computer capabilities; (2) although high and low pressure centers are well defined on long-term monthly mean pressure charts, this is not always the case on monthly charts for individual years. The location of the SH was always well defined. The AL was well defined in most Januaries but there were some years when it was a trough or area of low pressure extending from E to W over a large segment of the N Pacific. In these cases the location of lowest pressure was chosen subjectively. When the STH was not well defined the center of the protruding lobe of high pressure was chosen as the position of the STH. The 1951-83 mean position of the three pressure centers together with standard deviations and

Fig 4
Sea level pressure, January 1958, upper panel; 1969, lower panel



extremes are listed in Tab 1. Years when the AL was split into an E and W cell were not included in these calculations but the locations of these cells fell within the range of the AL listed in Tab 1.

The important result of this preliminary investigation is the small variance in the latitude and longitude of the SH, the STH, and in the latitude of the AL relative to the large variance in the longitude of the AL. The longitude of the AL, remaining near 50°N, largely determines the sea level atmospheric pressure pattern. This behavior of the AL simplifies development of indices which will depend primarily on its longitude and pressure.

Indices of Atmospheric Pressure Distribution Patterns

A number of curve fitting procedures, using grid point values of analyzed fields, are available to aid in examining the year to year differences in the zonal distribution of pressure at lat. 50°N. One convenient procedure is harmonic analysis. If the analysis is restricted to the first harmonic which is a simple sinusoidal fit, then only three values in the function

$$S(x) = A(0) / 2 + C(1) \cos (w (x-P(1))) \qquad (1)$$

describe the gross pressure distribution along the latitude band: A (0) / 2 is the mean pressure;

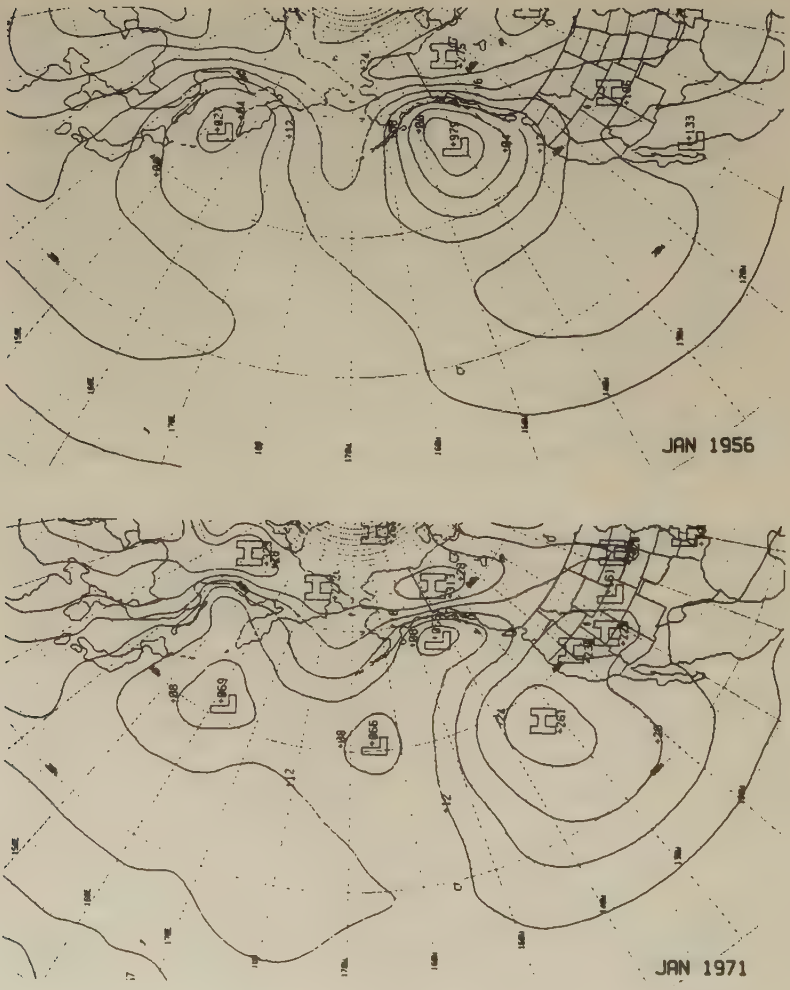


Fig 5
Sea level pressure, January 1956, upper panel; 1971, lower panel

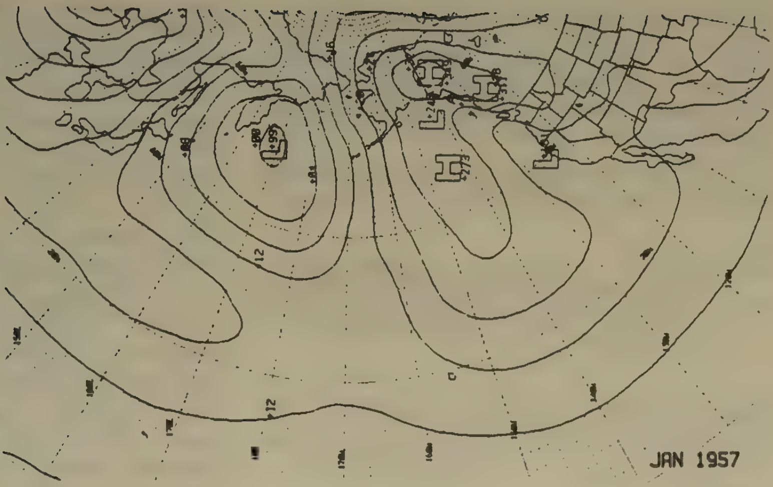


Fig 6
Sea level pressure, Januar 1957

C (1) is the amplitude reflecting the magnitude of the pressure change along the latitude band; and P (1), the phase angle, in this application reflects the zonal displacement of the minimum pressure. The segment of the latitude band to be analyzed determines the value of w. The variable x is the longitude.

In this exploratory investigation the harmonic analyses were performed using the grid values of the winter (December, January, February) sea level pressure fields for 1947 to 1972, of Namias (1975) together with the updates to 1985 which were kindly provided by Dr. Namias. The grid values at lat. 50°N are 10° of longitude apart. The latitude band analyzed ranged from long. 150°E, in the Sea of Okhotsk, to 130°W near the Canadian coast. The assumed wavelength, then, is 80 degrees of longitude with x = 0 at long. 150°E and x = 8 at long. 130°W.

Results of the analyses which were carried out to the second harmonic, are listed in Tab 2. The fitted curves for selected years are shown in Fig 7 to 11. Normalized anomalies of A (0), C (1), and P (1) are shown in Fig 12.

Of interest in Tab 2 are the amplitudes, C (1), and the phase angles, P (1). All values of C (1) are positive except those for 1950, 1956, and 1969. The negative values indicate a phase shift of half a wavelength and mean that high pressure is found at the longitudes where low pressures normally occur. These years are those with a blocking ridge such as that illustrated in Fig 5.

The average phase angle, excluding the blocking ridge years, is -0.9. This means that the minimum of the sinusoid is 9 degrees of longitude to the W of mid-wave (170°W) or at 179°W. Again excluding the blocking ridge years, all but two phase angles are negative. These years are 1958 and 1983, the pronounced El Niño years, when the minimum of the sinusoid is shifted E of mid-wave to 162° and 161°W, respectively.

Fig 7 to 11 illustrate how well the harmonic curves fit the grid point values of pressure. The distribution of pressure across the Pacific at 50°N is not harmonic and consequently relatively large departures of the analytic curve from the grid values are to be expected. The largest departures tend to be at 150°E and 130°W. When these

Tab 1
1951-83 mean position, standard deviation, and extremes of the Aleutian Low, the Siberian High, and the N Pacific Subtropical High

	Mean	Std. Dev.	Extremes	
Aleutian Low	50° N 179° W	3.8 14.9	59° N 157° E	41° N 150° W
Siberian High	48° N 97° E	1.9 5.0	51° N 90° E	46° N 108° E
Subtropical High	32° N 132° W	5.0 6.6	48° N 158° N	24° N 121° W

two positions, located in the Sea of Okhotsk and near the E boundary of the Pacific, are excluded then the simple sinusoid (solid line) explains between 80 and 90% of the variance. The analytic curve which includes the second harmonic (dotted line) improves the fit and explains 85 to 95% of the variance.

An example of the blocking ridge years is shown in Fig 7. The zonal distribution of pressure for the pronounced El Niño years of 1957/58 and 1982/83 in which the eastward shift of lowest pressure is clearly evident, are shown in Fig 8 and 9. An example of the westward shift of lowest pressure which also is the blocking ridge year 1969, is shown in Fig 10. Finally Fig 11 for 1971 is an example when the AL was not well defined.

Tab 2 Constants in the function for the distribution of sea level pressure at 50°N between 150°E and 130°W, $S(x) - 1000 = A(0) / 2 + C(1) \cos(w(x-P(1))) + C(2) \cos(w(2x-P(2)))$ mb, for each winter of 1947 to 1985. $w = 360 / 8$, $x = 0$ at long 150°E, $x = 8$ at long. 130°W

Year	A (0)	C (1)	P (1)	C (2)	P (2)
1947-72 mean	10.0	3.7	-1.2	1.6	-0.4
1947	15.4	4.6	-1.5	1.4	-0.8
1948	10.8	5.4	-1.2	1.7	-0.6
1949	18.5	7.4	-1.9	2.1	-1.0
1950	19.8	-6.4	1.5	1.2	-1.2
1951	21.1	2.8	-1.7	1.4	0.2
1952	12.6	3.5	-2.0	1.1	0
1953	-1.2	6.1	-0.2	1.5	-0.2
1954	9.6	3.9	-0.3	1.7	-0.4
1955	13.0	6.2	-1.5	1.8	-1.0
1956	18.6	-4.4	0.1	1.6	0
1957	18.5	7.6	-1.4	1.1	-1.4
1958	0	4.3	0.8	2.7	0.5
1959	8.8	2.7	-0.6	2.9	-0.4
1960	3.8	5.8	-0.9	1.6	-0.9
1961	-2.4	5.5	-0.3	2.2	-0.8
1962	15.0	5.6	-1.5	1.4	-1.0
1963	5.8	5.6	-0.5	2.3	-0.9
1964	0.6	7.9	-0.2	2.2	-0.8
1965	9.2	4.1	-1.6	1.8	-0.4
1966	7.2	4.9	-1.8	1.5	-0.2
1967	2.8	4.6	-1.5	2.0	0.2
1968	9.1	2.7	-1.7	2.0	-0.5
1969	15.1	-4.0	1.3	0.8	1.4
1970	-4.1	6.9	-0.1	2.2	-0.4
1971	14.4	1.7	-1.0	0.6	-1.2
1972	19.1	4.0	-1.8	0.9	0.4
1973	9.1	3.3	-1.1	1.9	-0.9
1974	3.8	3.7	-0.9	1.6	-0.9
1975	7.2	4.8	-0.6	1.4	-0.5
1976	5.6	5.2	-0.7	1.9	-1.2
1977	-7.0	11.4	-0.4	3.2	-0.9
1978	-0.8	5.4	-0.5	2.0	-0.2
1979	13.6	6.0	-1.4	1.5	-0.9
1980	6.1	3.7	-0.6	2.2	-0.8
1981	-0.4	7.9	-0.1	1.2	-1.3
1982	15.5	2.5	-1.7	1.1	-0.6
1983	-7.1	7.8	0.9	2.4	0.3
1984	6.8	4.0	-0.9	3.0	-0.9
1985	11.2	7.6	-1.0	1.6	-1.1

The analysis is based on data from Namias (1975) plus updates

The normalized anomalies for 1947 to 1985 of the mean pressure, A (0), the amplitude, C (1), and the phase angle, P (1) are shown in Fig 12. The calculations for the anomalies of P (1) do not include those for the blocking ridge years of 1950, 1956, and 1969. Although anomalies in the mean atmospheric pressure at lat. 50°N are presented in Fig 12A, they are not important in terms of wind driven currents. The anomalies in the amplitude (Fig 12B) are important, however, and not necessarily related to the mean pressure. There were seven years with an amplitude of more than one standard deviation above average, indicating higher than average geostrophic winds. Amongst these years 1977, with an amplitude more than three standard deviations above average, stands out. There were seven years with an anomaly of more than one standard deviation below average, meaning that winds associated with the AL were below average also.

Anomalies in the phase angle (Fig 12C) reflect the E-W shifts in the longitude of the AL. These shifts determine over what portion of the N Pacific winds will have a northerly or southerly component in the direction of flow. There were two outliers, one in 1958 and the other in 1983, when the lowest pressure was displaced eastward by more than two standard deviations from the mean longitude. All together, there were six years when the anomalous position was one or more standard deviation to the E and seven years when it was more than one standard deviation to the W of the mean location.

Representations of the atmospheric pressure distribution along 50°N as in Fig 7 to 11, can be used to infer qualitative information about the zonal distribution of pressure gradients, particularly when the second harmonic is added in generating the curves. The first derivative of the analytic expression gives the distribution of the zonal pressure gradient, excluding the E and W sides of the latitude band where the harmonic fit is not good. It is simpler, however, to obtain pressure gradients directly from the grid point values of the analyzed monthly or quarterly pressure distributions produced by meteorological services.

Indices of the Large-Scale Wind Distribution

Wind systems associated with the AL are the northwesterlies to the W, the southwesterlies to the E and the westerlies to the S of the AL. Indices of components of these winds are the large-scale pressure gradients between the longitude at 50°N of the AL and 160°E, near Kamchatka, and the longitude of the AL and 130°W, near the Canadian coast. The westerly index is the pressure gradient between 50°N and 25°N at the longitude of the AL. The gradients together with the distances between the location of the AL and the W and E reference locations, and the longitude of the AL are listed in Tab 3. The data source was, as before, the winter grid values of Namias (1975).

Fig 13 shows the normalized anomalies in the northerly (panel A), southerly (panel B), and westerly (panel C) components of the wind, W, E, and S of the AL, respectively. The anomaly in the longitude of lowest pressure along 50°N is shown in Fig 13D. The northerlies are only a part of the large wind system associated with the pressure gradient between the SH and the AL that affects E Siberia as well as the W portion of the N Pacific. The most frequent longitude of the AL from 1947 to 1985 was 170°E (Tab 3). With an average longitude, for the same years, at 176°E less than 20% of the latitude band over the Pacific was under the influence of the northerly wind component. Anomalies in this wind component, therefore, primarily affect the W boundary region of the ocean.

The anomaly of the southerly wind component E of the AL was more than one standard deviation higher than average during six years. These winters included the pronounced El Niño years of 1958 and 1983 as well as that of 1977. The southerly wind component was more than one standard deviation weaker than average in 1956 and 1969, the blocking ridge years.

The westerly indices depend upon the pressure of the AL and that of the subtropical ridge in the central part of the ocean, S of the AL. Variation in the latter is small in comparison to the former so that again, the pressure of the AL is the dominant factor in the pressure gradient. There were five winters with winds one standard deviation stronger than average. The largest positive anomalies occurred in 1977 and 1983. The westerlies were weakest in 1956, a blocking ridge year, and in 1971, and 1982 when the amplitude of the pressure variation along 50°N was small.

Fig 13D shows that there were six years with anomalous displacements of the AL to the E by more than one standard deviation. The largest anomalies occurred during the pronounced El Niño years of 1958 and 1983. The largest westward displacements occurred during the blocking ridge years of 1950, 1956, and 1969.

The direction of displacement of the AL in Fig 13D agrees with that in Fig 12C except during three years when the anomaly was small. The outlier years, 1958 and 1983, appear as such in both representations. The other outlier years are those with a blocking ridge which show as the largest westward displacements in Fig 13D. These years were anomalous also in the harmonic analysis but were not plotted in Fig 12C.

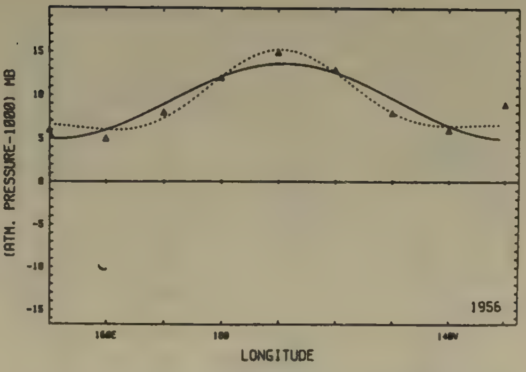


Fig 7 Harmonic fit, winter 1956, of sea level pressure between 160°E and 130°W at 50°N: first harmonic solid line; first plus second harmonic, dashed line. (See text and Tab 2.) Triangles are grid values from Namias (1975)

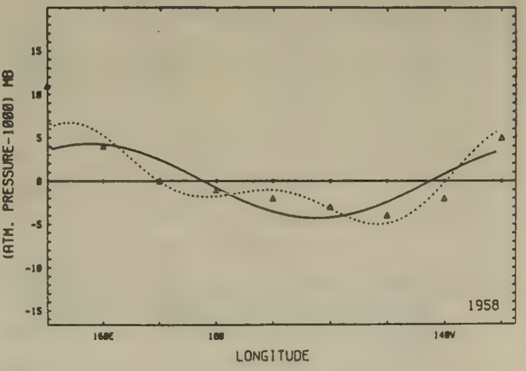
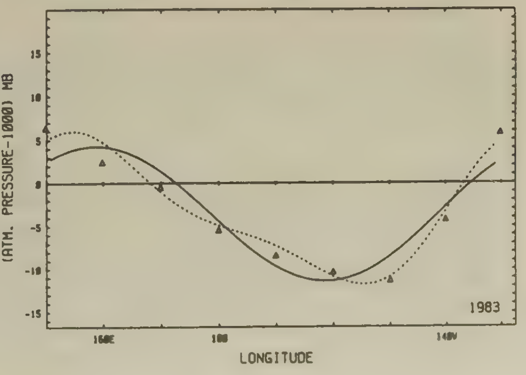


Fig 8 Same as Fig 7. Winter 1958

Fig 9 Same as Fig 7. Winter 1983



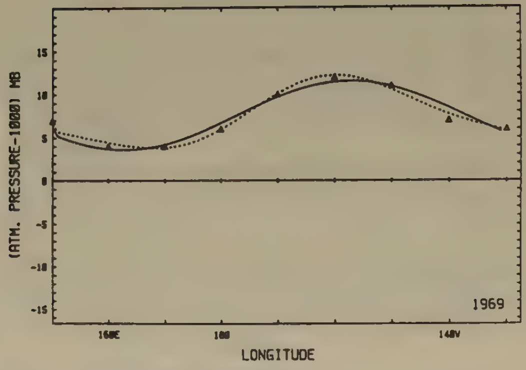


Fig 10 Same as Fig 7. Winter 1969

Fig 11 Same as Fig 7. Winter 1971

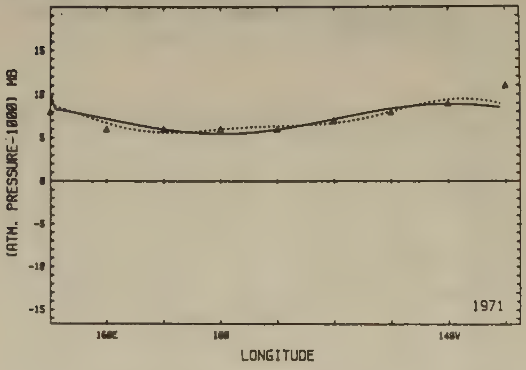
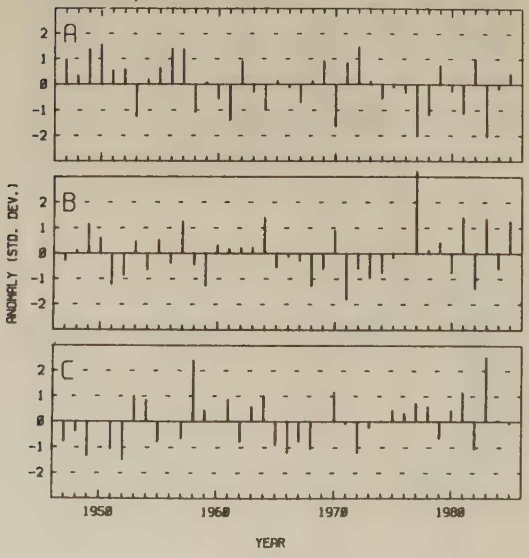


Fig 12 Normalized anomalies, winters 1947 to 85, of harmonic constants: panel A, the mean pressure at 50°N, A (0) / 2; panel B, the amplitude, C (1); panel C, the phase angle, P (1). (See text and Tab 2 for details)



The Strength of the Wind Systems

Normally the section of the N Pacific under the influence of the northerly wind component is small. This influence may not be small, however, during years when the AL is displaced eastward of its normal position. In the transfer of energy from ocean to atmosphere through evaporation, not only is the magnitude of the wind speed important, but also the area of ocean under the influence of the wind. Also in biological considerations, the area as well as the intensity of a wind system may be important. An index that reflects both intensity of the wind and area of influence can be obtained by multiplying the pressure gradient by an index of the area. For purposes of this exploratory investigation, I used as the area index the square of the distance between the same high and low pressures as were used to calculate the gradient. The gradient times area index, the "strength" of the wind system, for the northerly and southerly wind components is listed in the last two columns of Tab 3 labeled S1 and S2. The anomalies of the strength are plotted in Fig 14.

Fig 14A shows that the strength of the wind system W of the AL was near or slightly below average (less than one standard deviation) during most winters. During seven years this index was near one or more standard deviations higher than average. The highest anomalies of more than two and four standard deviations occurred during 1958 and 1983, respectively. During these years the AL was displaced to the E of its normal position and in most of the same years the pressure gradient was higher also.

Fig 14B shows that the strength of the wind system E of the AL was weakest during 1958 and 1983. The strength of this system can also be weaker than average when the amplitude in the pressure distribution at 50°N is low as it was in 1971 or when there is a blocking ridge in the central Pacific as it was in 1956 and 1969. The strength of the system was more than two standard deviations higher than the mean during 1977. During this year the amplitude of the pressure distribution at 50°N was the highest of the 39 winters shown.

Discussion

From this exploratory investigation it is clear that characteristics of winter sea level atmospheric pressure distributions over the mid-latitude N Pacific can be quantified in terms of wind indices. These indices, in turn, can be used to identify years with anomalous pressure distributions. One method of deriving indices involves fitting a sinusoid to the sea level pressure distribution along 50°N. This is an elegant method because only three constants are required to quantify the distribution (Tab 2). The

Year	L1	G1	L2	G2	G3	X (2)	S1	S2
1111	707	-2.83	4242	2.59	-5.64	170	-1.41	46.67
1947	707	-1.41	4242	2.83	-4.54	170	-0.71	50.91
1948	707	-4.24	4242	3.54	-6.54	170	-2.12	63.64
1949	707	-1.41	4242	3.30	-6.00	170	-0.71	59.39
1950	0	.00	4949	1.82	-5.09	160	.00	44.55
1951	707	-2.83	4242	1.89	-4.91	170	-1.41	33.94
1952	707	-1.41	4242	1.65	-5.64	170	-0.71	29.70
1953	2121	-3.30	2828	4.95	-8.54	190	-14.85	39.60
1954	1414	-2.12	3535	2.55	-5.27	180	-4.24	31.82
1955	707	-2.83	4242	3.30	-6.18	170	-1.41	59.39
1956	0	-2.83	4949	0.81	-3.27	160	.00	19.80
1957	707	-5.66	4242	3.30	-4.91	170	-2.83	59.39
1958	3535	-2.26	1414	6.36	-7.64	210	-28.28	12.73
1959	707	-2.83	4242	2.59	-6.18	170	-1.41	46.67
1960	1414	-2.12	3535	4.53	-7.64	180	-4.24	56.57
1961	1767	-2.26	3181	5.03	-7.64	185	-7.07	50.91
1962	707	-2.83	4242	3.06	-4.36	170	-1.41	55.15
1963	1767	-1.70	3181	5.34	-4.73	185	-5.30	54.09
1964	2121	-3.77	2828	7.07	-8.73	190	-16.97	56.57
1965	707	-1.41	4242	2.59	-5.64	170	-0.71	46.67
1966	707	-1.41	4242	2.83	-7.64	170	-0.71	50.91
1967	707	-2.83	4242	3.30	-7.64	170	-1.41	59.39
1968	707	.00	4242	2.36	-5.27	170	.00	42.42
1969	353	.00	4595	0.44	-5.09	165	.00	9.19
1970	2121	-3.30	2828	6.36	-8.73	190	-14.85	50.91
1971	1767	.00	3181	1.57	-3.27	185	.00	15.91
1972	707	-2.83	4242	1.65	-4.36	170	-1.41	29.70
1973	707	-1.41	4242	2.36	-6.73	170	-0.71	42.42
1974	707	-1.41	4242	2.83	-5.45	170	-0.71	50.91
1975	1414	-2.83	3535	3.39	-6.54	180	-5.66	42.42
1976	1414	-1.41	3535	4.24	-6.54	180	-2.83	53.03
1977	1767	-5.66	3181	8.80	-10.18	185	-17.68	89.09
1978	1414	-3.53	3535	3.96	-7.82	180	-7.07	49.49
1979	707	-2.83	4242	3.30	-6.36	170	-1.41	59.39
1980	707	-2.83	4242	2.59	-5.82	170	-1.41	46.67
1981	2121	-5.18	2828	7.07	-7.82	190	-23.33	56.57
1982	707	.00	4242	1.41	-4.18	170	.00	25.45
1983	3535	-3.96	1414	11.31	-10.00	210	-49.49	22.63
1984	707	.00	4242	3.54	-5.45	170	.00	63.64
1985	1414	-2.83	3535	5.37	-5.82	180	-5.66	67.17

Tab 3 Indices of winter wind systems. X (2) is the longitude of lowest pressure at 50°N. L1 and L2 are distances in km between X (2) and 160°E and X (2) and 130°W. G1, G2, and G3 are the pressure gradients in 1000 mb/km, W, E, and S of the AL (see text). S1 and S2 are indices of the strength of the wind systems in .001 mb.km, W and E of the AL (see text). X (2) < 180 is E, X (2) > 180 is 360-X (2) W. Year 1111 is the 1947-72 mean winter

sinusoidal fit is a first order approximation and not good near the W and E sides of the latitude band analysed. Nevertheless, the amplitude of the sinusoid is a good index of the magnitude of the pressure variation or "intensity" of the AL and therefore also of the associated wind systems. Important also is the year-to-year variation in the longitude of the AL. This characteristic is reflected by the phase angle of the sinusoid. The major anomalies in the longitude of minimum pressure such as occurred in 1958 and 1983, are indicated without uncertainty by the phase angle but there is uncertainty, particularly in the magnitude of the phase angle anomaly, when displacements are in the range of one standard deviation or less.

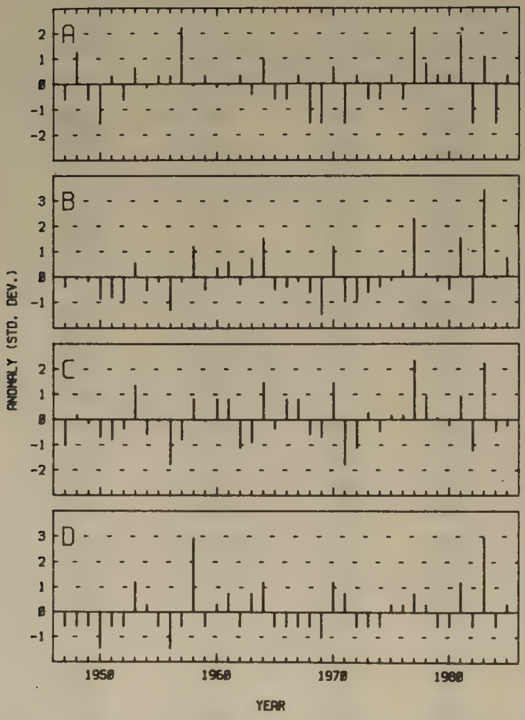
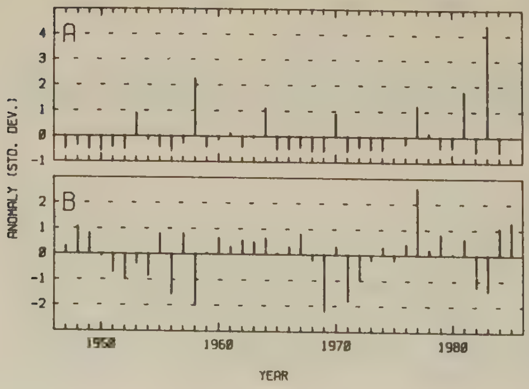


Fig 13 Normalized anomalies, winters 1947 to 85, of pressure gradients, panel A, between 160°E and AL at 50°N; panel B, between 130°W and AL at 50°N; panel C, between 25° and 50°N at longitude of the AL. Panel D, normalized anomalies of the longitude of the AL. (See text and Tab 3)

Fig 14 Normalized anomalies, winters 1947 to 85, of the strength index: panel A, wind system W of the AL; panel B, wind system E of the AL. (See text and Tab 3)



The second harmonic in the harmonic analysis materially improves the fit, particularly in terms of the longitude of minimum pressure. However, there are now five constants required to describe the distribution and the advantage of simplicity is lost.

A more direct way to obtain indices of the wind systems that are associated with the large-scale pressure distributions is to calculate the pressure gradient directly from the grid values of the pressure field. Only five variables are necessary to calculate six indices: (1) the longitude and (2) the pressure of the lowest pressure along lat. 50°N, the pressures at (3) the W and (4) the E reference positions, and (5) the pressure of the subtropical ridge at lat. 25°N and the longitude of minimum pressure at lat. 50°N. The indices are the longitude of the AL, the overall pressure gradients associated with the northerly and southerly wind components W and E of the AL, respectively, and of the westerly wind S of the AL (Tab 3). Additionally, there are the "strength" indices of the northerly and southerly wind systems W and E of the AL (Tab 3). These indices reflect the combination of wind intensity with area of influence of the wind systems, highlighting different aspects of the wind systems.

One shortcoming of these large-scale indices is that the detail in the zonal distribution of the gradient between the AL and the E and W boundaries is obscured. An example that may be important in some applications is the longitude of the maximum southerly wind component. A second shortcoming is that the years with a blocking ridge in the central portion of the ocean are not identifyable in the large-scale gradient analysis although these years appear as a large anomaly in the harmonic analysis.

A relatively frequent occurrence in the pressure distribution over the N Pacific is an area of high pressure over the E side of the ocean such as occurred in 1957 (Fig 6). This type of anomalous distribution also is not clearly reflected by the indices derived from either method. It is a simple matter, however, to calculate zonal pressure gradients between grid locations and so obtain both the longitude of highest gradient and indication of anomalous high pressure in the E N Pacific.

Modern statistical techniques and analyses of meteorological fields can be used to derive indices of the wind field that are useful in oceanographic applications. These techniques are not necessarily available to those investigating biological distributions that may be affected by large-scale anomalies in wind systems. Gridded values of monthly mean sea level pressure distributions on a finer scale than were used here are produced by meteorological services. These data are available to compute either monthly or quarterly values of the simple indices described.

El Niño and Longitude of the Aleutian Low

In his paper "Teleconnections from the equatorial Pacific" Bjerknes (1969) was the first to draw attention to the effects on the mid-latidude atmospheric circulation of the anomalously warm episodes in the central equatorial Pacific. Rowntree (1972), using a Geophysical Fluid Dynamics Laboratory model, tested and confirmed Bjerknes' hypothesis that the Aleutian low would deepen and shift eastward as a consequence of the anomalous equatorial warming. Figs 12C and 13D show that the outlier years in the eastward displacement of the AL were 1958 and 1983, the major equatorial warm episode (El Niño) years. In 1983 the AL deepened and the westerly index was more than two standard deviations above average, also. In 1958 the AL deepened and the southerly index E of the AL was more than one standard deviation above average. The westerly index, however, was less than one standard deviation above average (Fig 13C). The Bjerknes hypothesis holds during most of the lesser El Niño years as defined by Quinn et al. (1978) but there are exceptions. For example, the 1972 event was not reflected by the mid-latitude indices. In 1981, according to the indices shown in Fig 13, the AL was deeper and displaced eastward and the westerly and southerly indices were more than one standard deviation above average, but there was no El Niño. In 1977 when the AL was the deepest, the eastward displacement was less than one standard deviation above average.

Anomalous Wind Systems and Oceanographic Implications

An interesting result of the 1976/1977 NORPAX satellite tracked drift buoy experiment is shown in Fig 15 (McNally 1981). The buoy displacements from the beginning to the end of the month when plotted on the mean sea level atmospheric pressure charts for December 1976, January, February, and March 1977, show that the drift was parallel to the isobars and changed with the changing isobar pattern. From this result one can infer that the surface currents would be different and also anomalous during the years with anomalous pressure distribution patterns. McNally (1981) calculated that a certain wind and drift vector relationship holds for winds above 2.5 m/s. One can conclude from this result that there may be a threshold geostrophic wind above which the buoy displacement and isobar relationship is as during the drifter experiment.

Fig 16 shows the drifting buoy pattern when wind speeds are less than 2.5 m/s as during the summer. Such a variable pattern is also to be expected during the winter months when atmospheric pressure gradients are small. Example years are 1971, those with a blocking ridge in the central Pacific, and those when high pressure dominates the E side of the ocean.

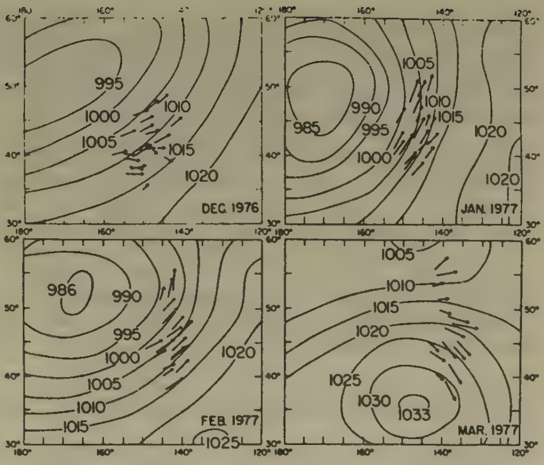
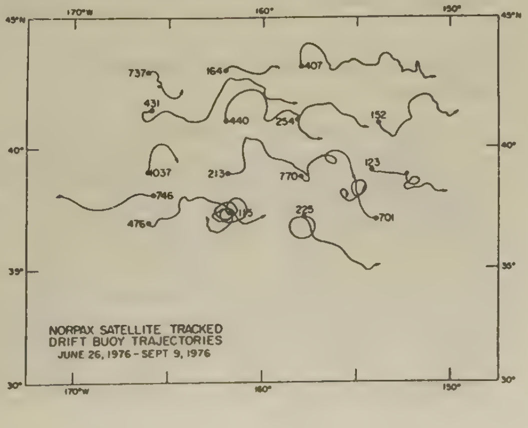


Fig 15 Drifter positions superimposed on monthly mean sea level pressure charts. The arrows indicate monthly displacements of individual drifters (McNally 1981)

The NORPAX drift buoy experiment took place during the winter of 1977 when pressure gradients were the highest in the 39 years examined here. There may have been other unique aspects to the circulation during this winter that caused the relationship between monthly isobar patterns and drifter direction. There is an element of uncertainty, therefore, when the drifter results are extrapolated to other years. This uncertainty can be resolved with additional drifter experiments.

Anomalous large-scale wind systems also affect other oceanographic processes, particularly those that change the sea surface temperature. The

Fig 16 Trajectories of drifters for the period June 1976 through September 1976. Solid dots indicate initial positions; solid triangles indicate last position (McNally 1981)



effects on the sea surface temperature of some of these such as those produced by the mixing of the surface water or by evaporation are difficult to determine with the data available here. The effect of advection on the sea surface temperature, however, is direct. During the winter sea surface isotherms, other than near the E and W boundaries, are approximately zonal in direction and therefore advection is most sensitive to changes in the meridional component of the wind driven surface current. The large-scale anomalies in the magnitude and direction of the pressure gradients, particularly E and W of the AL are expected to produce significant anomalies in the sea surface temperature distribution.

Anomalous Wind Systems and Climate Implications

Anomalous evaporation rates affect the atmosphere as well as the ocean because the atmosphere's primary source of energy is that latent in water vapor. During most years the longitude of the AL is in the W Pacific (Tab 3 and Fig 13D). This probably means that over a major portion of the mid-latitude N Pacific anomalies in evaporation rates are not so much a function of the difference between the saturation vapor pressure at the sea surface and the vapor pressure of the air as of anomalies in the wind speed. This situation changes, however, when the AL is displaced eastward and a relatively larger section of the latitude band comes under the influence of an air mass with a lower vapor pressure and, consequently, a higher vapor pressure difference. Although the increase in evaporation rate may be small, the increased area over which the higher evaporation rate takes place can significantly increase the total gain of energy of the atmosphere. The strength index (Fig 14) reflects this effect which is most pronounced during the El Niño years, such as 1958 and 1983. This conjecture must be verified, of course, by calculating the total evaporation over the appropriate areas of the mid-latitude N Pacific.

Anomalous Wind Systems and Biological Implications

The linkages between environmental anomalies and biological processes and distributions are most difficult to establish. Bakun and Parrish (1980) have described the difficulties and the progress that has been made in E boundary current regions. These difficulties equally apply to the open ocean regions. In terms of large-scale systems, Parrish, Nelson, and Bakun (1981) have related reproductive strategies of coastal fisheries species to major features in surface transport. For example, in the mid-latitude coastal region of the E N Pacific coastal fish species having pelagic larvae tend to spawn during winter when the surface wind drift is generally directed toward the coast. The winds responsible for the onshore drift are a part of the large-scale winter wind system and therefore also affected by its anomalies. Anomalies affecting the onshore drift are those occurring when high pressure dominates the E N Pacific and the maximum zonal pressure gradient has shifted westward. The onshore drift is also affected by the magnitude of the gradient associated with an eastward shift of the AL into the Gulf of Alaska.

In the proceedings of a meeting on the effects of the 1982/83 El Niño on the E subarctic Pacific (Wooster and Fluharty 1985) papers describe and attempt to link the environmental anomalies with biological distributions. It would be interesting to examine in the same manner years with a blocking ridge in the central Pacific (1950, 1956, 1969) or those with high pressure in the E Pacific such as 1957.

In the central Pacific little is known about the effect of the large-scale environmental winter anomalies on biological processes. Do these anomalies affect the subsequent spring bloom? Is the distribution and abundance of salmon and albacore forage affected? Do the inferred anomalies in the wind driven circulation affect the movement, distribution, and migration of salmon and albacore? What are the effects of anomalies in the size and location of the highest pressure gradients E of the AL?

There are wind related indices of importance to biological processes that cannot be derived from large-scale mean pressure distributions. A turbulent mixing energy indexc is an example.

Conclusion

The objective of this study has been to identify quantitatively various characteristics of the large (thousands of km) scale pressure systems that are obvious from inspection of monthly or quarterly charts and no attempt has been made to discuss their meteorological significance. J. Namias, a pioneer in extended weather forecasting, was the first to study associations in the anomalies of N Pacific sea surface temperature, atmospheric pressure and climate and has published numerous articles on the subject in meteorological journals.

There are limits to the information that can be extracted from large-scale pressure distributions. However, indices are still needed and can be derived, of the longitude and width of highest gradients E of the AL and of the anomalous condition when high pressure dominates the E N Pacific.

Only a few anomalous pressure distributions have been identified: 1. The zonal pressure gradient is anomalously low as in 1971, or high as in 1977. 2. The AL is displaced into the E N Pacific. 3. There is a blocking ridge in the central Pacific as in 1956. 4. High pressure dominates the E Pacific as in 1957. 5. Lowest pressure is shifted westward. This shift may be associated with either condition 3 or 4. Indices of these large-scale anomalies may be used to classify the effects of wind forcing on ocean processes and circulation and on biological processes and distributions. Eventually it may be possible to predict the oceanographic consequences of the large-scale anomalies.

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THE FEEDING HABITS OF TWO DEEP SLOPE SNAPPERS, *PRISTIPOMOIDES ZONATUS* AND *P. AURICILLA*, AT PATHFINDER REEF, MARIANA ARCHIPELAGO

The lutjanid snappers belonging to the genus *Pristipomoides* are among the most prized and valuable commercial fish resources in tropical and subtropical regions of the Pacific Ocean (Polovina and Ralston 1987). These fishes normally inhabit escarpments with high vertical relief. During an intensive bottom fish survey conducted at Pathfinder Reef in the Mariana Archipelago, two species of snappers, *P. zonatus* and *P. auricilla*, comprised more than 68% of the total catch (Polovina 1985). Depth of capture data on these two species demonstrated overlap in their bathymetric distribution (Polovina et al. 1985; Ralston and Williams 1988).

Numerous feeding studies have been conducted on snappers that inhabit shallow (<100 m) water; however, published information on the diets of deep slope snapper species in the tropical Pacific is nearly nonexistent (see review by Parrish 1987). Kami (1973) noted prey items for four species of *Pristipomoides* in Guam with total sample sizes ranging from one to six individuals, and Kluegel (1921) presented information on the diet of *P. filamentosus* in Hawaii based upon four fish. The present paper examines how two coexisting species, *P. zonatus* and *P. auricilla*, partition food resources. With recent efforts to expand and develop commercial fisheries for tropical snappers as well as other deep dwelling bottom fishes, there is an increasing need to recognize the resources that support these fishes. The results presented here will therefore be useful for developing fishery management strategies and will lead to a better understanding of the ecology of tropical demersal communities.

Methods

Stomach and spew samples from 106 *P. zonatus* and 72 *P. auricilla* were collected at Pathfinder Reef during an intensive fishing experiment on 10–19 April and 5–7 May 1984. Located in the Mariana Archipelago at lat. 16°30′N, long. 143°05′E, Pathfinder Reef is a circular, volcanic pinnacle rising to about 16 m beneath the surface. The fishes, ranging from 30.2 to 44.4 cm fork length ($\bar{x}$ = 38.4 cm, standard deviation = 2.81), were caught with hook and line on hydraulic-powered gurdies. The terminal rig and gurdy specifications are described in Uchida and Uchiyama (1986). While fishing, the vessel was usually allowed to drift over the banks and steep slopes, targeting species in the 150–275 m depth range. Our study species were captured mainly in depths between 180 and 220 m. Fishing was conducted around the entire perimeter of the bank during daylight hours (Polovina 1986).

Typical of feeding studies conducted on deepwater species with swimbladders, regurgitation of stomach contents posed serious problems (Bowman 1986). The rapid ascent to the surface forced most of the stomachs to evert and lose an unknown quantity of the contents. Many food items, however, were caught in the throat or gill rakers, picked out, and saved. These items, referred to as spews, and full stomachs were frozen and returned to the laboratory for analysis.

Laboratory procedures for examination of the samples were similar to those employed by Harrison et al. (1983). Briefly, food samples were sorted, counted, and identified to the lowest practical taxon. The volume of prey items was measured by water displacement. Fishes were predominantly identified by osteological and external anatomical characters and morphometrics. Invertebrates were identified by undigested hard parts and external morphological features including shells for gastropods and exoskeletons for crustaceans.

To analyze the data, we used percent frequency of occurrence to provide a qualitative picture of the food spectrum and percent volume of prey to describe relative biomass of prey items (Hyslop 1980). Because a high percentage of the diets was composed of urochordates, we did not employ any numerical analysis of the prey items. These pelagic, colonial tunicates (all *Pyrosoma* spp.) did not occur in discrete units and were thus difficult to count.

An interspecific comparison of the two snapper species requires some measure of diet overlap and niche breadth. Diet overlap (C_λ) was computed by using the formula developed by Morisita (1959) and modified by Horn (1966). C_λ is formulated as

$$C_\lambda = \frac{2 \sum_{h=1}^{s} p_{ih} \cdot p_{jh}}{\sum_{h=1}^{s} p_{ih}^2 + \sum_{h=1}^{s} p_{jh}^2};$$

where p_{ih} and p_{jh} are the biomass proportions of a prey item h in the diets of species i and j, respectively, and s is the total number of major prey taxa in the food spectrum. C_λ varies from zero, when there is no overlap between the diets of species i and j, to one, when all prey items are in equal proportions. Niche breadth (B) for each species was computed by using the formula developed by Levins (1968):

$$B_i = \frac{1}{\sum_{h=1}^{s} p_{ih}^2};$$

where again, p_{ih} is the biomass proportion of a prey item h in the diet of species i and s is the total number of major prey taxa. The breadth values range from one, when prey items consist only of one category, to s, when all food items are in equal proportion in the same diet. These breadth values were then normalized as $B_n = B/s$, which ranges from a value of zero, representing the most uneven distribution of prey composition in the diet, to one, representing a totally even distribution. For the calculation of both breadth and overlap indexes, only prey items identified at least to the family level were used.

Results

The diets of *P. zonatus* and *P. auricilla* differed considerably from each other (Table 1). By volume, the 106 food samples from *P. zonatus* collected for this study were composed of 59.0% invertebrates and 41.0% fishes. The dominant invertebrate prey included the pelagic tunicate *Pyrosoma* spp. and galatheid crabs, nearly all *Munida japonica*. The most frequently occurring fishes in the diet were the ophichthid eel, *Shultzidia johnstonensis*, and the symphysanodontids *Symphysanodon maunaloe* and *S. typus*. In general, *P. zonatus* preyed heavily upon benthic organisms. Many of the prey items, such as echinoderms, octopods, and the various benthic crustaceans, must have been captured at the substratum. Conversely, the 72 food samples from *P. auricilla* were composed of 88.2% invertebrates and 11.8% fishes by volume; all were predominantly pelagic forms. Major invertebrate prey included the pelagic heteropod *Atlanta* spp., the pelagic tunicate *Pyrosoma* spp., and numerous species of cavolinid pteropods. Few fishes, most of them small and unidentifiable, were eaten by this snapper species.

The dietary overlap value (C_λ) was calculated to be 0.04. Based on the Langton (1982) convention of 0.00–0.29 as the low overlap, 0.30–0.60 as the medium overlap, and >0.60 as the high overlap, very little overlap occurred between the diets of the two snappers at Pathfinder Reef.

The niche breadth values (B) calculated for the two species indicated *P. zonatus* had a higher food breadth (3.82, $s = 10$) than *P. auricilla* (2.05, $s = 6$), suggesting more food specialization among the latter. Evenness in the proportion of the diet attributed to each prey type, however, was similar for the two species ($B_n = 0.38$ in *P. zonatus*; $B_n = 0.34$ in *P. auricilla*).

Discussion

As previously mentioned, a few fragmentary reports (cf. Parrish 1987) from various localities have addressed the trophic relationships of any tropical snapper inhabiting waters deeper than 100 m. He further attributes this lack of information to the normally remote fishing localities and, most of all, to the loss of stomach contents through regurgitation during capture.

The problem of regurgitation has plagued trophic studies of demersal fishes, regardless of whether fishing involved trawls (Mauchline and Gordon 1984; Clark 1985; Bowman 1986) or hook and line (Kluegel 1921; Forster et al. 1970; Seki 1984). Likewise, most food samples for our study were salvaged, regurgitated spewings retained in the mouth, throat, or gill rakers of the fishes. It is possible that the material occurring as spews may consist predominantly of certain prey items more likely retained because of size or some morphological structure, thereby resulting in a biased interpretation of the diet. We nevertheless employ the assumption that what is recovered is representative of the diets at the time of capture.

Based upon depth of capture information, *P. zonatus* and *P. auricilla* occupy nearly the same habitat, and considerable spatial overlap occurs in their foraging zones (Polovina 1986; Ralston and

Williams 1988). During submersible dives at Johnston Atoll, Ralston et al. (1986) verified this cohabitation with visual observations of the two species. *Pristipomoides zonatus* were observed between 215 and 250 m (median, 230 m) and *P. auricilla* between 205 and 295 m (median, 240 m). Our dietary analysis suggests that these two demersal species partition food resources by selecting prey from different microhabitats. *Pristipomoides zonatus* is best described as a demersal carnivore, with its diet containing benthic and demersal invertebrates together with tunicates and small fishes. In contrast, *P. auricilla* feeds primarily on large pelagic plankton, as evidenced by the abundance of heteropods, pteropods, and tunicates among the prey items. Kami (1973) also found tunicates (*Pyrosoma* spp.) in four of the five *P. auricilla* food samples in Guam. The differences in diet composition are consistent with the suggestion, based upon catch rates and the taking of a baited hook, that *P. zonatus* is the more aggressive predator of the two species (Polovina 1986).

Although our study revealed little overlap between the diets of *P. zonatus* and *P. auricilla*, the common occurrence of *Pyrosoma* spp. in the diets of both species seems significant. Similarly, these tunicates were also found among the stomach contents of three other congeneric species (Kami 1973; Parrish 1987). Kashkina (1987) reported intensive predation on pyrosomes, as well as salps, among

TABLE 1.—Diet composition of *Pristipomoides zonatus* and *P. auricilla* at Pathfinder Reef, Mariana Archipelago.

Species	*Pristipomoides zonatus* (*N* = 106)		*Pristipomoides auricilla* (*N* = 72)	
	% volume	% frequency	% volume	% frequency
Invertebrates				
Hydrozoa				
Siphonophora	—	—	3.2	20.8
Ctenophora	0.3	0.9	—	—
Polychaeta	0.3	0.9	5.4	15.3
Gastropoda	0.1	0.9	0.3	4.2
Atlantidae	—	—	0.9	12.5
Cavolinidae	0.2	4.7	38.1	72.2
Cephalopoda	0.3	0.9	7.4	2.8
Teuthoidea	—	—	0.2	1.4
Octopoda	0.1	0.9	—	—
Crustacea	2.6	10.4	5.5	44.4
Stomatopoda	0.3	0.9	0.3	1.4
Euphausiacea				
Euphausiidae	—	—	0.7	4.2
Decapoda				
Caridea	0.5	2.8	0.3	2.8
Pandalidae	1.2	2.8	—	—
Palinura	—	—	0.7	1.4
Anomura				
Galatheidae	19.6	28.3	—	—
Brachyura	17.1	13.2	0.2	1.4
Echinodermata				
Ophiuroidea	0.1	0.9	—	—
Tunicata				
Pyrosomatidae	16.3	34.9	25.0	37.5
Fishes				
Osteichthyes				
(Unid. fishes)	16.3	22.6	8.7	16.7
Anguilliformes	8.2	7.6	—	—
Ophichthidae	8.6	10.4	—	—
Myctophiformes	—	—	2.5	1.4
Ophidiiformes				
Ophidiidae	0.1	0.9	—	—
Perciformes				
Serranidae	4.0	1.9	—	—
Symphysanodontidae	3.1	5.7	—	—
Chaetodontidae	0.1	0.9	—	—
Gempylidae	—	—	0.6	2.8
Tetraodontiformes				
Balistidae	0.6	0.9	—	—

numerous pelagic and demersal fish species. Originally thought to be of little nutritional value, these tunicates have been found to contain filtered concentrations of phytoplankton and microzooplankton, thereby elevating the preys' food value. Regional and highly localized oceanographic processes will affect the distribution of such potential planktonic prey, and exploitation of these resources may influence the local distribution of predator species (Brock and Chamberlain 1968; Bray 1981). Deepwater snappers are most abundant on slopes of upcurrent exposure and near underwater headlands at Johnston Atoll (Ralston et al. 1986). These abundance patterns were attributed to planktonic concentrations created by mesoscale oceanographic processes as noted with other fishes on bank or slope habitats (Isaacs and Schwartzlose 1965; Pereyra et al. 1969).

Polovina (1986) suggested that fishing may selectively deplete one species, such as *P. zonatus*, preferentially over another (*P. auricilla*) and thereby alter the species composition in a given locality. With the small degree of dietary overlap between the two species in this study, such selective removal of *P. zonatus* will decrease predation pressure on the demersal prey resources of this species and, as evidenced in Larson (1980), may ultimately allow greater niche breadth for coexisting predator species.

In conclusion, this study has provided qualitative insight into dietary habits of two sympatric, deepwater species and has permitted some inferences regarding their ecology. Much more study is needed to comprehend fully the role of these predators in the ecosystem. Logistical constraints, including the problem of regurgitation, will continue to make quantitative assessments of diet a difficult task until new capture methodologies are developed. However, the rewards in improved understanding of deepwater ecology and increased ability to manage these valuable stocks suggest that the efforts will be justified.

Acknowledgments

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Striped Bass Populations in Chesapeake and San Francisco Bays: Two Environmentally Impacted Estuaries

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Striped bass populations have declined precipitously in both Chesapeake Bay and the San Francisco Bay Delta system.

Parallel declines in both systems indicate possible common climatic patterns or trends affecting both populations. Climatic instability on both coasts with accompanying changes in average rainfall, outflow and temperature may be interacting with deteriorating water quality and pollution resulting in declining populations of striped bass in both areas. Declines in east coast striped bass stocks have been attributed to: overfishing; nutrient enrichment of the habitat and the resultant, temperature-oxygen squeeze on subadults; deterioration of the near-shore habitat for juvenile striped bass resulting from the loss of submerged aquatic vegetation; decreased survival of larval striped bass due to environmental pollution; poor nutritional state of larvae; and fluctuations in the physical environment and predation.

In the San Francisco Bay Delta area the decline has been attributed to the interactive effects of reduced freshwater outflow and increased freshwater diversion, and decreased bay flushing and increased pollutant burdens which have adversely affected both egg production and egg and larval survival.

The striped bass, *Morone saxatilis*, is an anadromous species distributed along the Atlantic coast from northern Florida to the St. Lawrence Estuary, Canada, and along the Gulf of Mexico from western Florida to eastern Louisiana. The San Francisco Bay Delta population of striped bass originated in New Jersey. Juvenile striped bass from the Navesink River were introduced into the lower Sacramento River in 1879; additional yearlings from the Shrewsbury River were planted in San Francisco Bay in 1881 (Setzler *et al.*, 1980).

Striped bass spawn in late spring. In the Chesapeake Bay area spawning occurs from early to mid-April through to the end of May, primarily in tidal freshwater areas just above the salt wedge. Chesapeake Bay and its tributaries (Fig. 1a) provide the principal spawning and nursery areas along the Atlantic coast. The Chesapeake stock may comprise as much as 90% of the Atlantic coastal migratory stock of striped bass during periods of peak abundance (Berggren & Lieberman, 1978).

In the San Francisco Bay Delta area spawning occurs above the salt-wedge (or null zone) from mid-April through mid-June primarily in the Sacramento River and the central delta of the San Joaquin River, the major tributaries of San Francisco Bay (Fig. 1b).

Striped bass populations have declined for the past decade over much of their East Coast range, especially in Chesapeake Bay. Both commercial and recreational fisheries depend upon the occurrence of periodic dominant year classes to sustain population levels (Florence, 1980). The last dominant year class in 1970 resulted in peak commercial landings in 1973 (Boreman & Austin, 1985). Maryland landings declined from 2268 t in 1973 to 202.3 t in 1983 (Maryland Department of Natural Resources, 1986). Current stock levels are so low that the State of Maryland issued a total moratorium on the catch, sale or possession of striped bass in Maryland effective 1 January 1985.

As on the east coast, the San Francisco Bay striped bass have declined over the last 20 years, particularly since the drought of 1976–1977. The decline has been surprisingly similar to that in Chesapeake Bay as reflected in similar downward trends in young-of-the-year (YOY) survival in the two areas (Fig. 2a & b).

Stevens *et al.* (1985) have hypothesized four possible reasons for the decline of the San Francisco Bay fishery:

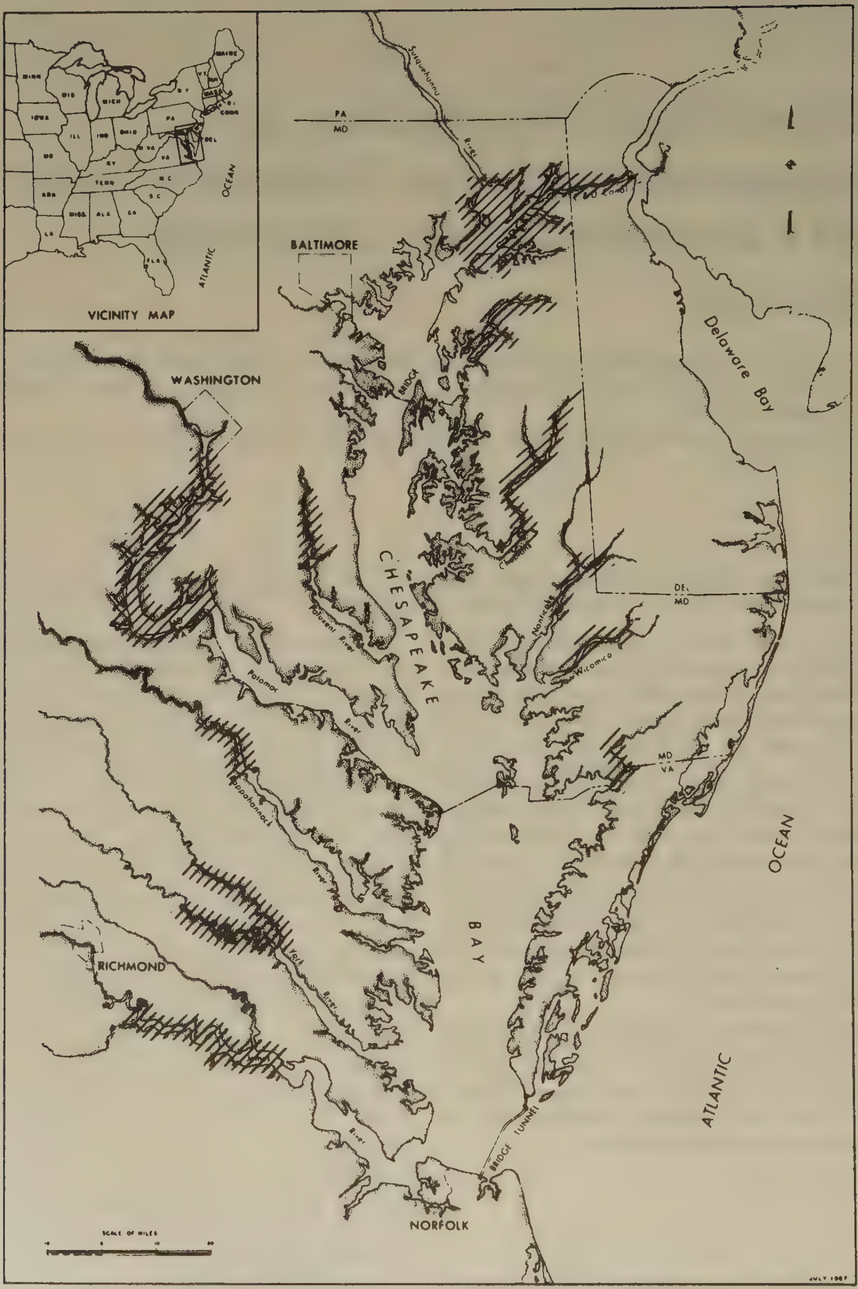
VICINITY MAP
ATLANTIC
OCEAN
BALTIMORE
WASHINGTON
RICHMOND
NORFOLK
PA
MD
DEL
MD
MD
VA
Susquehanna River
Canal
Delaware Bay
BRIDGE
Patuxent River
Potomac River
Rappahannock River
York River
River
Nanticoke
Wicomico
CHESAPEAKE
BAY
BRIDGE TUNNEL
ATLANTIC
OCEAN
SCALE OF MILES

Fig. 1A Spawning areas of striped bass in Chesapeake Bay and its tributaries.

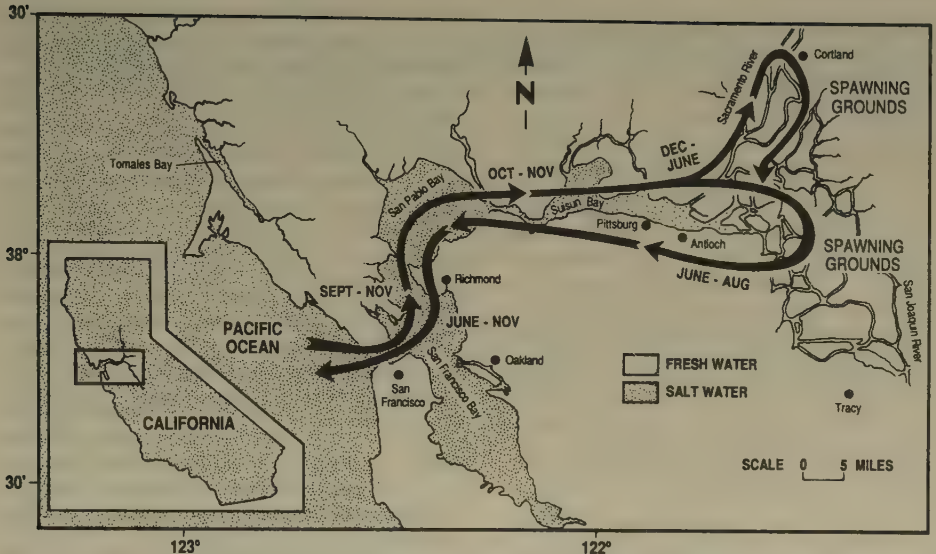
30'
38°
30'
123°
122°
Tomales Bay
PACIFIC OCEAN
CALIFORNIA
San Pablo Bay
Suisun Bay
San Francisco Bay
Richmond
Oakland
San Francisco
Pittsburg
Antioch
Cortland
Tracy
Sacramento River
San Joaquin River
N
SEPT - NOV
OCT - NOV
JUNE - NOV
DEC - JUNE
JUNE - AUG
SPAWNING GROUNDS
SPAWNING GROUNDS
FRESH WATER
SALT WATER
SCALE 0 5 MILES

Fig. 1B Spawning areas and spawning migration of striped bass in the San Francisco Bay Delta estuary.

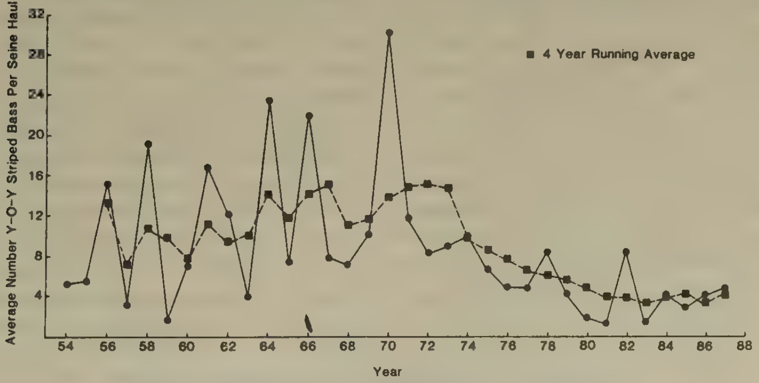

Fig. 2A Average number of YOY striped bass per seine haul from Maryland waters of Chesapeake Bay. This number is commonly referred to as the "Maryland Juvenile Index".

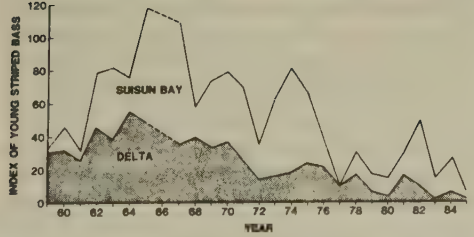

Fig. 2B Annual index of YOY striped bass by area in the Sacramento–San Joaquin Estuary. The young-of-year index is based on the catch per net tow when the average fork length of YOY striped bass reaches 38 mm. (Stevens *et al.*, 1985).

1. increased adult mortality resulting in low egg production, *2.* reductions in the planktonic prey of young striped bass in the western Sacramento-San Joaquin Delta and Suisun Bay during the spring, *3.* substantial losses of young fish by entrainment in water diversions, and *4.* physiological stress to the population by toxic substances such as petroleum hydrocarbons and pesticides.

Recent analysis by the California Department of Fish and Game (CDF&G, 1987) suggests the decline is probably due to a combination of increased adult mortality, lowered total fecundity affecting the total survival of YOY and decreased survival of eggs and very early larval stages (prior to 6 mm). Food abundance for older larvae may be less important than previously thought since it appears that mortality of eggs and larvae less than 6 mm has a greater effect on YOY recruitment than mortality of later stages (Low, 1986; CDF&G, 1987).

Unlike Chesapeake Bay, excessive water temperatures, low oxygen concentrations, and low pH do not appear to be major problems for San Francisco Bay

Delta populations of striped bass, although some larvae are lost to power plant entrainment (Chadwick, 1977). Overfishing is probably not a major factor contributing to the decline of striped bass in the San Francisco Bay Delta area (Stevens *et al.*, 1985).

There are levels of toxic pollutants in both Chesapeake and San Francisco Bay Delta areas and their tributaries, which are potentially harmful, including several petroleum and chlorinated hydrocarbons and trace metals (Jung *et al.*, 1984; Gunther *et al.*, 1987; Phillips, 1987). Research in San Francisco Bay (Whipple *et al.*, 1987; Jung *et al.*, 1984) has shown relatively high concentrations of many pollutants in tissues of striped bass. There are significant correlations among pollutants and reductions in reproduction and effective fecundity in striped bass, as well as evidence of effects on the adults.

This article examined the role of environmental degradation and pollution in the decline of Chesapeake Bay and San Francisco Bay striped bass stocks.

Overview of Chesapeake Bay Studies

Chesapeake Bay is a highly eutrophic, partially mixed, stratified estuary (see e.g. Kemp *et al.*, 1983; Officer *et al.*, 1984; Price *et al.*, 1985; Tuttle *et al.*, 1987). A major loss of submerged vegetation involving both native and exotic species has continued in Chesapeake Bay since the mid 1960s. Kemp *et al.* (1983) demonstrated that recent losses in Bay vegetation were linked to increased eutrophication and ultimately to light stress. Reduction in seagrass beds result in habitat loss for both finfish and epibenthic invertebrate populations (Orth & Heck, 1980; Heck & Orth, 1980). Shorezone fishes (such as juvenile striped bass) generally prefer naturally vegetated bottoms over bare bottoms (Briggs & O'Connor, 1971); such areas provide abundant food supply and protection from predators (Orth, 1977).

Coutant (1985) has hypothesized that adult striped bass are 'squeezed' from Chesapeake Bay during summer months because of their thermal and dissolved oxygen preferences or requirements. The thermal niche of striped bass decreases as the fish ages. Maximum growth rate of 1 yr-old juveniles occurs at 24–26°C (Cox & Coutant. 1981); whereas striped bass >5 kg (age 3+) prefer 20–22°C and avoid water temperatures >25°C and dissolved oxygen concentrations <2–3 mg l^{-1} (Coutant, 1985, 1987).

The deep, mesohaline waters of Chesapeake Bay have experienced annual summer anoxia or hypoxia since at least 1936 (Tuttle *et al.*, 1987). Based on a 30 yr old O_2 record for Chesapeake Bay. Officer *et al.* (1984) concluded that the summer volume of water having oxygen concentrations <0.5 mg O_2 l^{-1} increased approximately 15-fold between 1950 and 1980. If low dissolved oxygen (DO) concentrations have reduced striped bass habitat sufficiently to influence reproductive success than one would expect that upper Bay (Maryland rivers) striped bass would be more significantly impacted than lower Bay stocks (Virginia rivers). However, both upper and lower Bay stocks have suffered severe declines. Since a large portion of adult striped bass (primarily females) are migratory, the impact of the dissolved oxygen squeeze on reproductive success is questionable. Female striped bass do not mature sexually until ages 5, 6, and 7 yr; however, immature female striped bass begin migrating at 2 yr; approximately 50% of immature female striped bass leave the bay at 3 yr and join the coastal migratory stock (Kolenstein, 1981). These coastal migrants do not return to the Bay until they are sexually mature and participate in the spring spawning migrations. Gill net surveys indicate that more 2 yr old immature females leave the Bay than previously thought (Harley Speir, Maryland Department of Natural Resources, personal communication). Whether this is related to the temperature-oxygen squeeze as Coutant (1985) hypothesized, or to the reduction in fishing mortality of 2 yr old males after the imposition of the striped bass moratorium is open to question. Prior to the moratorium, sexually mature 2 and 3 yr old males experienced high fishing mortality during the spring spawning migration; immature females did not participate in spawning migrations to any great extent and thus were subjected to a smaller fishing mortality. Higher fishing mortality among 2 yr old males together with some migration of immature 2 yr old females could result in the approximately even sex ratios of 2 yr old striped bass seen in gill net surveys conducted prior to the total ban on fishing imposed by the moratorium.

Upper Chesapeake Bay stocks of all anadromous fish species are currently experiencing severe declines (Bonzek & Jones, 1984; Stagg, 1985). However Chesapeake Bay populations of marine spawners; i.e. bluefish and the various sciaenids; Atlantic croaker, spot and weakfish (sea trout) have not undergone similar declines. This implies that environmental impacts are likely to be operating primarily in the tributary rivers and the tidal freshwater portion of the upper Bay, the spawning areas of the anadromous species.

There is increasing evidence that water quality in the traditional striped bass spawning areas of Chesapeake Bay may adversely affect spawning and survival of striped bass early life history stages. A mixture of organic and inorganic contaminants at realistic environmental concentrations (EC) was created from analyses of Choptank, Elk and Nanticoke River water in 1980 (CNFRL, 1983). This mixture significantly reduced survival of striped bass yolk-sac larvae (prolarvae) reared in soft water (Hall *et al.*, 1984).

Mehrle *et al.*, (1987) reported significant mortality of striped bass larvae reared in hard well water at 2 and 4X EC within 30 days. Larvae reared in low salinity waters were more tolerant of the contaminants. Striped bass larvae reared in 2 ppt salinity incurred significant mortality in the 4 EC treatment after 30 days of exposure; whereas significant mortality occurred in the 2 and 4 EC in 5 ppt after 90 days exposure.

Tests on metals and organics carried out separately (Palawski *et al.*, 1985) indicated that the acute toxicity of the mixture was largely due to metals, particularly zinc, cadmium and copper. Cadmium and copper were implicated in an *in situ* toxicity bioassay carried out during the spring of 1986 in the spawning reaches of the Potomac River (Hall *et al.*, 1987b). Poorly buffered eastern shore tributaries such as the Choptank and Nanticoke are particularly susceptible to episodic drops in pH, especially during wet years. It is likely that low pH with or without the potentiating influence of aluminium (Buckler *et al.*, 1987) may create toxic conditions in these rivers during the time of spring run-off which is also the beginning of striped bass spawning season.

The pH of rainfall in the Chesapeake Bay area averages 4.0 with individual events recorded as low as 3.0 (pH of 'normal' rainfall is 5.0–5.4 due to naturally occurring organic acids and CO_2 in the atmosphere (Maryland Department of Natural Resources, 1985)). Even during relatively dry springs pH values on the spawning grounds in Eastern Shore tributaries may be marginal. Average pH values for stations sampled in the peak spawning areas of the Nanticoke and Choptank Rivers during 1986 a dry spring, ranged 6.00–6.60 and 6.23–6.86, respectively (Setzler-Hamilton, 1987).

Hall *et al.* (1986) evaluated organic contaminants, toxic metals, and water quality parameters in 10 East Coast striped bass spawning habitats: Roanoke River; James, Pamunkey, Rappahannock, Potomac, Patuxent, Choptank, and Nanticoke Rivers—all tributaries of Chesapeake Bay; the C & D Canal; and the Hudson River. Most water quality conditions appeared adequate for prolarval survival. However, low buffering capacity of 24–28 mg l^{-1} $CaCO_3$ was found in the Roanoke, Pamunkey and Rappahannock Rivers. Burton (1982) reported 78.0% mortality for striped bass yolk-sac larvae after 4 days of exposure to soft water <34.6 mg l^{-1} $CaCO_3$ in the laboratory.

Potentially toxic concentrations of monomeric aluminium and copper were also found in various spawning habitats (Hall *et al.*, 1986). Monomeric aluminium concentrations ranging from 103–104 μg l^{-1} were reported from the Roanoke, James and Patuxent Rivers in the Chesapeake system as well as the Hudson River. A combination of 100 μg l^{-1} aluminium and a pH <7.3 is toxic to 31-day striped bass (Mehrle *et al.*, 1984). Copper concentrations of 11, 12, and 15 μg l^{-1} in the Potomac, Patuxent, and Rappanhannock Rivers respectively, also may have been toxic to striped bass yolk-sac larvae. These copper concentrations exceeded the 96 h LC_{50} of 7.2 μg l^{-1} reported by CNFRL (1983) and were of the same order of magnitude as the 96 h LC_{50} found by Wright (1988) (24.0 μg l^{-1} for 16 day old larvae at a pH of 8.3 reared in ideal conditions). Both monomeric aluminium and copper occurred at potentially harmful concentrations in the Patuxent (Hall *et al.*, 1986). It is interesting to note that during two years of intensive sampling of the Patuxent spawning grounds we caught only 12 striped bass larvae and 3 juveniles in 1978 (Setzler *et al.*, 1979) and no striped bass beyond the yolk-sac stage in 1979 (only 34 yolk-sac larvae 3–5 mm TL were caught) (Mihursky *et al.*, 1980).

Hall *et al.* (1987a) found significant *in situ* mortality rates of both yolk-sac and yearling striped bass in the Potomac. Survival of yolk-sac larvae ranged from 4.5–22.5% during three 96 h experiments; control survival was $\geq 81\%$. Yearling survival ranged from 0–77% during two 7 d experiments; highest mortality occurred at the upriver station and was probably due to a point source discharge. High concentrations of monomeric aluminium, cadmium and copper, acting singly or synergistically, were implicated together with sudden decreases in water temperature to <11°C. The peak concentration of monomeric aluminium, 90 μg l^{-1} found during these *in situ* experiments is potentially toxic (Mehrle *et al.*, 1984). Peak concentrations of cadmium, 7 μg l^{-1}, and copper, 72 μg l^{-1}, from the Potomac exceeded 96 h LC_{50}s of both cadmium, and copper (CNFRL 1983; Wright, 1988).

Wright (1988) exposed larval striped bass to copper and cadmium concentrations which were acutely toxic over a 96 h period (24 and 19 μg g^{-1} respectively) and to sublethal concentrations of these metals over a 3 week period. The distribution of copper concentrations in laboratory-exposed larvae (1–30 μg g^{-1} dry wt) was completely within the range of wild larvae (0.1–60 μg g^{-1} dry wt) from the Potomac and Choptank Rivers throughout the 1985 and 1986 spawning seasons. There was considerable overlap in cadmium frequency distributions from laboratory (range 0.5–27 μg g^{-1}) and field larvae (range 0.01–12 μg g^{-1} dry wt).

Body burdens of seven metals were measured in striped bass and white perch (*Morone americana*) larvae collected from weekly sampling of the Potomac, Choptank and Nanticoke spawning grounds (Wright, 1987, Table 1). Concentrations of aluminium increased in striped bass larvae from the Potomac and Nanticoke Rivers and concentrations of copper increased in striped bass larvae from the Choptank River during the 6 week sampling period; whereas concentrations of copper and manganese in the Potomac larvae, and manganese in the Nanticoke and Choptank larvae remained approximately the same (Wright, 1987).

The DDT metabolites, DDE and DDD were present in white perch larvae collected from the Potomac River in 1985; DDE was present in white perch larvae from the Potomac, Nanticoke and Choptank Rivers in 1986. Two striped bass samples were analysed in 1985; however, no DDT derivatives were found in either. Wright (1987) also found a number of organic contaminants in white perch larvae. The herbicide Atrazine (used extensively in no-till farming in Maryland) was found in concentrations of approximately 100 ng g^{-1} wet wt in white perch from three rivers; Potomac, Choptank, and Nanticoke during the third week of May in 1985. Simazine residues were also present (data from the Maryland Department of Agriculture documented use of 1.6 million pounds of Atrazine and 0.45 million pounds of Simazine in Maryland in 1985). Residues of the insecticide, Malathion; 71.0 ng g^{-1} were found in striped bass larvae ($n=26$ larvae in a pooled sample) and in two pooled samples of white perch larvae (145 and 123 ng g^{-1} respectively) collected from the Potomac River during May, 1985 (Wright *et al.*, 1986). However the toxicity of these compounds to larval striped bass are unknown at present.

TABLE 1

Concentrations of heavy metals in striped bass from the Chesapeake Bay and San Francisco Bay Delta estuaries. Tissue concentrations are in $\mu g\ g^{-1}$ dry wt except for CNFRL data and Mehrle *et al.* data where tissue concentrations are in $\mu g\ g^{-1}$ wet wt.

Source	Al	As	Cd	Cr	Cu	Mn	Ni	Pb	Se	Zn	Hg	Reference
Eggs												
Chesapeake Bay Tributaries												
Elk n=1*		0.16	0.003		2.0			0.012	0.13			CNFRL, 1983
Potomac n=1		0.3	0.014		4.4			0.017	1.8			
Choptank n=1		0.14	0.005		3.2			0.011	2.2			
Sacramento River		0.25	0.36		5.9			0.01	2.4			
Larvae												
Potomac 6 May 86 n=6	139±50.5		0.12±0.16	2.6±0.96	12.3±5.3	20.1±6.4		14.9±7.5		3200±4163		Wright, 1987
	34.9–196		0.03–0.48	1.4–4.45	5.1–19	14.1–29.9		2.8–24		160–12 300		
30 May 86 n=8	132±96		0.10±0.04	0.53±0.35	13.3±5.4	20.8±4.5		5.6±6.9		300±183		
	11–332		0.05–0.18	0.34–0.89	8.1–25.2	15.7–27.8		1.6–23.7		113–642		
Nanticoke 7 May 86 n=2	56–79		0.27–0.35	0.8–1.97	2.7–53.9	30.0		7.4–29.6		180–5500		
31 May 86 n=12	112±134		0.10±0.07	6.9±11.6	8.0±6.1	43±18		4.8±2.1		1800±4650		
	2.5–441		0.09–0.27	0.43–38.7	3.3–25.1	17–74		1.14–7.8		150–17 200		
13 June 86 n=8	183±65		0.14±0.09	0.71±0.19	8.4±2.7	27.7±6.7		1.1±0.6		126±19		
	81–225		0.04–0.34	0.45–1.02	5.3–13.4	19.6–38.6		0.1–1.9		90–154		
Choptank 8 May 86 n=3	1074±167		0.63±0.11	12.7±2.4	2.38±2.02	52.3±29.5		65.2±45.1		14 100		
	722–1445		0.29–1.1	5.8–21.6	0.94–3.8	22.9–81.8		24–128				
1 June 86	375±166		0.06±0.03	0.70±0.19	3.66±0.3	47.3±8.4		2.3±0.4		262±173		
	171–578		0.02–0.08	0.43–0.96	3.3–3.9	37.1–57.7		1.7–2.7		130–510		
Young-of-year												
Elk n=1	<0.4	0.16	0.02	0.36	0.88	7.2		0.08	1.3			CNFRL, 1983
Potomac n=2		0.16	0.009	0.3	1.09	6.1		0.06	0.72			
Choptank n=1	<0.6	0.15	0.013	0.34	0.94	7.6		0.04	0.37			
James n=1	<0.4	0.51	0.017	0.27	0.86	9.8		0.03	0.3			
Nanticoke n=1	<0.4	0.1	0.004	0.36	0.48	7.1		0.008	0.44			
Nanticoke n=5		0.13±0.01	0.05±0.01					0.73±0.01	0.19±0.01	39.20±4.02		Mehrle *et al.*, 1982
n=5		0.08±0.02	0.05±0.01					1.00±0.60	0.25±0.06	35.30±4.78		
n=5		0.40±0.03	0.05±0.01					0.67±0.15	0.64±0.03	32.66±4.29		
Potomac n=5		0.16±0.01	0.05±0.01					1.20±0.01	0.22±0.01	35.90±0.01		
n=5		0.20±0.19	0.05±0.01					1.34±0.73	0.66±0.14	55.48±2.05		
n=5		0.10±0.04	0.05±0.01					1.15±0.50	0.84±0.19	57.40±7.50		
Adults												
Elk n=1		0.84	0.15	0.85	1.34	3.00	0.14	0.12	0.69		0.07	CNFRL, 1983
Potomac n=1		0.55	0.40	0.90	1.47	3.33	0.23	0.16	0.60		0.09	
Choptank n=1		0.94	0.20	0.78	1.67	1.76	0.25	0.16	0.34		0.09	
Sacramento		0.38	0.15	0.84	1.46	2.09	0.26	0.19	0.48		0.27	

*Averages of duplicate pooled samples. All other YOY values represent results of a single pooled sample.

Table 2 summarizes concentrations of organic contaminants found in striped bass eggs, young-of-the-year (YOY) and adults from both Chesapeake Bay and San Francisco Bay. Concentrations of DDT derivatives and PCB's were higher in striped bass eggs than in either YOY or adults. (These organic contaminants are soluble in lipids; lipid storage in striped bass eggs is in a large oil globule.) Westin *et al.*, (1985) have demonstrated that hexachlorobenzene, chlordanes, DDTs and PCBs are passed from parent to the offspring via yolk and oil of the egg.

Reported 96 h LC_{50} concentrations of three organic insecticides to 56 day old striped bass are summarized below:

	Softwater Conc. μg l−1	1 ppt salinity μg l^{-1}
Toxaphene	5.4	7.6
Malathion	24.5	65
Carbaryl	760	2300

(From Palawski *et al.*, 1985).

The extreme toxicity of toxaphene to striped bass was not altered by water hardness whereas the toxicity of both malathion and carbaryl was reduced in water of 1 ppt salinity as compared to soft water.

The histopathology of larval striped bass has been examined in an attempt to identify causal relationships between specific water quality contaminants or stressors and the pathiology or death of larval fish. Examination of striped bass larvae, 5–7 mm TL, collected from the Choptank River during 1984 revealed severe liver and muscle damage at the cellular level; necrosis of liver cells and calcium deposition in adjacent muscle cells, indicative of pending mortality (Hall *et al.*, 1985). These results correlate with results of trawl studies in the Choptank; no larvae >7 mm were collected during the first 80% of the 1984 spawning season (Maryland Department of Natural Resources, 1985).

Hall *et al.*, (1987b) found lesions in the pseudobranch, dilated glomerular capillaries and vacuolization and eosinophilic inclusions in the proximal tubules of the kidneys (indicative of osmotic imbalance) of yearling striped bass exposed to Potomac River water. They also found reduced glycogen reserves in the livers of yearling striped bass from the C&D Canal (Hall *et al.*, 1987b).

Overview of San Francisco Bay Delta Studies

The severe decline of San Francisco Bay Delta populations of striped bass in the last 20 years probably results from interacting factors. The adult population of striped bass appeared to be relatively stable from about 1969 to 1976. Subsequently, adult abundance declined to about one quarter of that 20 years ago (Stevens *et al.*, 1985). Previously water diversion was implicated in reductions of the planktonic food supply and subsequent reduction in survival of young striped bass. Recent analyses (Low 1986; CDF&G 1987) have shown that survival to very young larval stages (from egg to 6 mm) is most important in determining the year-class strength. Accumulation of toxics in the ovaries of adult prespawning striped bass may result in increased mortality of eggs and delayed mortality of larvae prior to or at the time of first-feeding.

Field Studies

Striped bass from the San Francisco Bay Delta area have relatively high levels of several classes of petroleum hydrocarbons, chlorinated hydrocarbons and heavy metals (Tables 1–3; Whipple *et al.*, 1983, 1987, unpublished). Concentrations of monocyclic aromatic hydrocarbons (MAH), alicyclic hepanes (AH), and unmetabolized DDT in the livers and ovaries of prespawning striped bass from the San Joaquin and Sacramento Rivers from 1978–1984 were correlated to egg resorption, abnormal egg maturation and egg death. Striped bass from San Francisco Bay had higher percentages of egg resorption, at least in certain years, than striped bass from Coos Bay, Oregon, and Hudson River, New York, populations.

Crosby *et al.* (1986) found relatively high residues of chlorinated hydrocarbons, including PCBs, DDT and metabolites, and toxaphene in tissues of San Francisco Bay Delta striped bass. Residues were significantly higher than in Coos River, Oregon striped bass (Whipple *et al.*, 1983). PCBs in SF Bay striped bass were comparable to concentrations found in striped bass from the Hudson River (Gadbois & Maney, 1983). Although the mean concentration of PCBs was lower than from Hudson River fish (0.75 vs. 1.50 mg g^{-1} wet wt), the maximum concentration (4.0 mg g^{-1}) in muscle was the highest recorded in striped bass in this comparative study. The chlorinated hydrocarbon residues in particular, PCBs, DDT, and metabolites and toxaphene, were at levels potentially impacting the adult striped bass and their eggs and larvae (Crosby *et al.*, 1986; Jung *et al.*, 1984).

A number of investigators have found lesions in livers of adult striped bass containing high concentrations of chlorinated hydrocarbon residues (Crosby *et al.*, 1986). Brown *et al.* (1987) found significant liver dysfunction in moribund striped bass collected during a die-off in Carquinez Straits in the summer of 1985.

Whipple (unpublished) has found relatively high residues of petrochemicals (mean $[MAH]=2.39\pm6.90$ mg g^{-1}, wet wt, $n=9$ females) in livers and gonads of moribund, postspawning adult striped bass collected from the Carquinez Strait area in 1980. These concentrations were approximately 50 times greater than concentrations found in livers of prespawning adults in 1981 (mean $[MAH]=0.044\pm0.079$ mg g^{-1} wet wt; $n=19$ females).

Laboratory Studies

Concentrations of benzene in tissues of wild juvenile striped bass approximated those in tissues of juvenile striped bass exposed in the laboratory to 100 n l^{-1} benzene (Whipple *et al.*, 1981). Initial laboratory studies showed that benzene was primarily taken up through the gills and accumulated at highest levels in tissues with greatest lipid content (Korn *et al.*, 1976a). Effects of benzene exposure included changes in respiration (Brocksen & Bailey, 1973; Eldridge *et al.*,

TABLE 2

Summary of mean concentrations and ranges of whole body residues of organic contaminants in striped bass from the Chesapeake and San Francisco Bay Delta estuaries. Concentrations in $\mu g\ g^{-1}$ on wet wt basis.

Source	*n*	DDT	DDD	DDE	Total PCBs	Toxa-phene	Diel-drin	Chlor-dane	PAH[a]	PASH[b]	Total PCDDs[c]	Total PCDFs[d]	Non-*o*-PCBs[e]	Reference
Eggs	1[f]													
Potomac		0.03	0.1	0.48	4.0	ND[g]	0.06	0.23						CNFRL, 1983
Elk		0.05	0.33	0.6	3.91	0.24	0.05	0.61						
Choptank		0.1	0.54	1.08	6.19	0.55	0.07	0.88	144.0	1.5	12	51	+[h]	
Nanticoke									120.7	ND	3	44	28	
Sacramento		0.53	1.11	5.17	10.74	1.44	0.1	2.1			6	34	321	
Young-of-year	1[i]													CNFRL, 1983
Potomac		0.02	ND	0.02	ND	ND	ND	ND						
Elk		0.02	ND	0.05	ND	ND	ND	ND						
Choptank		ND	ND	0.02	ND	ND	ND	ND	28.5	ND				
Nanticoke		ND	ND	0.03	ND	ND	ND	ND	21.9	ND	6	2	ND	
Young-of-year														Mehrle *et al.*, 1982
Potomac	10				0.21±0.08									
	10				0.31±0.16									
	10				0.40±0.11									
Nanticoke	10				0.06±0.04									
	10				0.08±0.04									
	10				0.09±0.04									
Adult	1[j]													CNFRL, 1983
Potomac		0.07	0.06	0.31	2.2	0.5	0.02	0.39			2	55		
Elk		0.17	0.07	0.34	1.1	ND	0.01	0.18						
Choptank		0.11	0.10	0.41	2.5±1.5 (1.2–4.5, n=4)	0.2	0.04	0.39	284.0	5.1	25	23	92	
Nanticoke					2.8±0.3 (2.5–3.3, n=4)				241.2	28.7	19	25	40	
Sacramento		0.13	0.07	0.72	2.5	0.5	0.03	0.32			ND	26	42	

[a] PAH (polycyclic aromatic hydrocarbons)—Data are sum of concentrations of the 5 prevalent compounds (phenanthrene, fluoranthene, pyrene, benzo(*a*)fluorene, benzo(*a*)anthracene. All PAH data from one pooled sample of 4 individuals or egg masses.

[b] PASH (polyaromatic sulphur heterocycles)—Data are sum of concentrations of the 3 prevalent thiophenes (dibenzothiophene, phenanthro(4,5-*bcd*)thiophene, benzo(*b*)anaphtho(2,1-*d*)thiophene). All PASH data from one pooled sample of 4 individuals or egg masses.

[c] PCDD (polychlorinated dibenzofurans)—Data are sum of concentrations of compounds containing 4 to 8 chlorine atoms. All PCDD data are from one pooled sample of 3 individuals or egg masses.

[d] PCDF (dioxins)—Data are sum of concentrations of compounds containing 4 to 8 chlorine atoms. All PCDF data from one pooled sample of 3 indiviudal or egg masses.

[e] Non-*o* PCB (non-ortho substituted polychlorinated biphenyls)—Data are sum of concentrations of compounds containing 4 to 6 chlorine atoms. All non-*o* PCB data from one pooled sample of 3 individuals or egg masses.

[f] Data represent one pooled sample of eggs from 6–8 females.

[g] ND—Not detected.

[h] +—Detected, but concentration too low for accurate quantitation.

[i] Data represent one pooled sample of 4–6 individuals.

[j] Data represent one pooled sample of 6–8 adult females.

TABLE 3

Concentrations of selected pollutant classes in tissues of adult female prespawning striped bass (*Morone saxatilis*) from the San Francisco Bay Delta estuary (mean age = 5.9 yr; range = 4–20 yr). Concentrations in mg g^{-1} (ppm) wet wt for hydrocarbons, mg g^{-1} dry wt for metals. Data from Vasilleros *et al.*, 1982; Gadbois and Maney, 1983; Whipple, unpublished.

		Concentrations in tissues mg g^{-1}		
Pollutant Class				
Petroleum hydrocarbons		Liver	Ovaries	Muscle
Total monocyclic aromatics[*]	X±s n; Max	0.28±0.70 191; 10.0	0.23±1.21 187; 10.0	0.39±0.18 12;† 1.50
Total alicyclie hexanes‡		0.39±1.58 191; 5.0	0.56±6.17 187; 10.0	ND§
Total polycyclic aromatics		Whole fish composite 10.0		
Total naphthalenes		Whole fish composite 0.01		
Total thiophenes		Whole fish composite 6.0		
Chlorinated hydrocarbons				
Total DDT and metabolites		0.50±1.04 52; 1.57	2.61±3.72 12; 13.6	NM"
Chlordane		0.02±0.02 39; 0.12	NM	NM
Total PCBs		0.78±0.93 51; 5.00	2.64±2.62 12; 8.10	1.02±1.67 12; 4.00
Trace metals				
Cadmium		2.58±1.86 52; 9.40	0.23±0.22 12; 0.710	0.39±0.15 12; 1.30
Chromium		0.44±0.67 52; 3.30	0.95±0.52 12; 2.20	1.24±0.38 12; 2.20
Copper		61.6±60.3 52; 220	5.63±1.96 12; 35.0	2.00±3.36 12; 3.36
Lead		0.21±0.08 12; 0.370	0.180±0.23 12; 0.89	0.23±0.13 12; 0.62
Mercury		1.99±2.04 52; 13.0	0.183±0.20 12; 0.96	0.22±0.,19 12; 1.60
Nickel	X±s n; Max	1.26±0.42 12; 1.80	0.98±0.48 12; 2.10	1.40±0.41 12; 2.00
Selenium		7.28±3.70 45; 21.0	NM	NM
Zinc		160±52. 52; 272	61.0±49.2 75; 310	21.0±31.3 12; 66.0

[*] Benzene, toluene, ethylbenzene, *o*-, *p*-, *m*-xylenes.

† Mostly toluene.

‡ Cyclohexanes, methyl cyclohexane. isomers of dimethyl cyclohexanes.

§ ND = not detected

" MM = not measured

1981), alterations in growth and fat content (Korn *et al.*, 1976b), abnormal hatching and larval development (Eldridge *et al.*, 1981), decreased effective fecundity and reproduction (Whipple unpublished), abnormalities in organs and tissues (Taberski, 1982) and increased serum cortisol and secondary stress responses (MacFarlane & Benville, 1986).

Discussion

It is interesting to note that the decline in YOY striped bass follows a similar pattern in the two areas. Survival in the San Francisco Bay Delta is significantly correlated to survival in Maryland Waters of Chesapeake Bay ($r = 0.568$; $p = 0.0023$; Table 4). A simple method of the first difference transformation was applied to reduce the possible effects of autocorrelation on the abundance trends (Bakun & Parrish, 1980). Preliminary examination shows the trends persist after the transformation. We feel that further analysis and investigation of the possible causes of these common trends would be interesting.

At this time, the tertiary factors which may be responsible for affecting populations similarly in both areas are unknown. Both coasts have experienced unstable climatic conditions in the last 10 years when compared to the more stable preceding 20 years. In the San Francisco Bay area, for example, there has been a warming trend for the past 10 years (1975–1985; Dowgiallo *et al.*, 1986). During that period, a drought (1976–1977) and a significant El Niño event (1982–1983) have occurred. This climatic instability also relates to the variability in rainfall, riverflow and temperatures on both coasts.

The Chesapeake Bay area experienced colder than normal winters in 1977 and 1978. A major drought occurred during 1985 and 1986 and summer temperatures during 1987 reached record highs. Kerr (1985) showed data confirming observations of erratic winter weather and temperatures in the Continental United States for the eight years 1976–1984. In contrast, the preceding 20 years (1955–1975) were characterized by stability of winter temperatures. Periods of stability may be related to the good year classes of striped bass in the 1960s, and early 1970s in San Francisco Bay and 1970 in Chesapeake Bay, while recent instability may relate to recent downward trends.

There was no significant correlation between YOY

TABLE 4

Correlation analysis of young-of-the-year (YOY) survival indices for Maryland rivers vs. San Francisco Bay Delta and Suisun nursery areas (1959–1985). All data was transformed to natural logarithms. YOY indices from San Francisco Bay Delta area defined in Stevens *et al.* (1985); data from Maryland rivers are average catch per seine haul (Md. Dept. Nat. Res. 1986).

YOY Index	n	Correlations YOY Delta		YOY Suisun		YOY Total, California	
		r^2	Prob.	r^2	Prob.	r^2	Prob.
Delta	27			0.1640	*	0.6873	‡
Suisun	27	0.1640	*			0.6693	‡
Total California	27	0.6873	‡	0.693	‡		
Nanticoke	27	0.3815	‡	0.2527	†	0.4035	‡
Choptank	27	0.1519	*	0.2106	*	0.2057	*
Head-of-Bay	27	0.2528	†	0.0801	n.s.	0.2391	†
Potomac	27	0.0166	n.s.	0.0013	n.s.	0.0062	n.s.
Mean Maryland River	27	0.3491	‡	0.1572	*	0.3223	†

*Significant at $p < 0.05$
†Significant at $p < 0.01$
‡Significant at $p < 0.001$
n.s. Not Significant

recruitment in the San Francisco Bay Delta and YOY recruitment in the Potomac River in contrast to YOY recruitment in the upper Bay, Choptank, Nanticoke and Maryland waters as a whole (Table 4). The correlation of YOY recruitment success in upper Chesapeake and San Francisco Bays implies a common climatic influence on recruitment success.

Salinity regimes in the striped bass spawning region of the Potomac (≈ 100–170 km upriver from the mouth) are primarily controlled by freshwater input from the upper Potomac instead of freshwater input to the upper Bay. One would anticipate that global climatic events would exert a greater influence on the freshwater input to Chesapeake Bay from the Susquehanna River which drains most of Pennsylvania and central New York and supplies 90% of the freshwater to the upper Chesapeake Bay than on the freshwater input to the Potomac which has a more localized drainage area (western Maryland and the Appalachian region of northern Virginia and West Virginia).

Body burdens of some petroleum and chlorinated hydrocarbons in both populations of striped bass (Table 2) are at levels which can affect striped bass condition, growth, reproduction and survival. Highest mean concentrations of DDD and DDE were found in striped bass eggs from the Sacramento (1.1 and 5.2 μg g^{-1} wet wt., respectively) and the Choptank Rivers (0.5 and 1.1 μg g^{-1}) which are surrounded by agricultural lands. Concentrations of total PCBs in the two systems were also highest in striped bass eggs from the Sacramento (10.7 μg g^{-1}) and Choptank (6.2 μg g^{-1}) Rivers (Table 2). Concentrations of PCBs were higher in striped bass eggs from the Hudson River, 26.4 μg g^{-1}, (CNFRL, 1983). Although total PCB concentrations in adult female striped bass from the Hudson were higher than in adult females from either the Chesapeake or San Francisco systems, concentrations were of the same order of magnitude (7.6 μg g^{-1} in Hudson vs. 1.1–2.8 μg g^{-1} in the Chesapeake and San Francisco estuaries). Concentrations of organic hydrocarbons were typically higher in striped bass from the Sacramento River than in striped bass from Chesapeake Bay tributaries (Table 2).

Survival of both starved and fed striped bass larvae in laboratory experiments was inversely related to concentrations of chlorinated hydrocarbons; HCB, DDTs, PCBs and chlordanes) in the eggs. Body burdens of chlorinated hydrocarbons increased in rough proportion to the cumulative amount of food-borne contaminant (*Artemia* nauplii containing distinctive organochlorine residues) in striped bass larvae hatched from eggs with low maternal contributions of chlorinated hydrocarbons. In larvae with high initial concentrations of contaminants however, only DDTs showed accumulation during the feeding period (Westin *et al.* 1985).

A further comparison of Chesapeake and San Francisco Bays shows other similarities and differences. High spring flows appears important to survival of striped bass in the San Francisco Bay Delta and the Potomac estuary. Stevens *et al.* (1985) found that outflow was the major factor associated with survival to YOY stage in the San Francisco Bay Delta population. In years of high flow striped bass larvae are transported down estuary to Suisun Bay where abundant populations of zooplankton prey are found. Higher than normal spring flows (April only), along with colder-than-normal winter temperatures are also correlated with successful year classes in the Potomac River (Boynton *et al.*, 1977; Mihursky *et al.*, 1981). However this relationship does not appear to hold for the upper Chesapeake Bay (Walter Boynton, CBL, pers. comm.).

Polgar *et al.* (1985) evaluated the effects of climatic factors, human population changes and dredging activity on Potomac River striped bass stocks (1929–1976). Climatic factors, specifically previous December's temperature, April temperature and April river flow most significantly affected striped bass population dynamics; pollution variables were not significant. In contrast Potomac River stocks of American shad showed strong dependence on human population levels (but not on dredging activity) compared to climatic factors (Polgar *et al.*, 1985).

Low pH and fluctuations in pH adversely affect populations of striped bass in the low conductivity, freshwater Eastern Shore tributaries of Chesapeake Bay (Hall *et al.*, 1985). In these tributaries, metals and organics input are via the pulses of freshwater resulting from precipitation. Thus for example, although the rainfall in the Choptank River watershed during the 1986 spawning season was insufficient to produce a pulse through the system, one minor storm producing ~0.5 in. of rain resulted in a two fold increase in monomeric aluminium in the spawning reaches of the river (Maryland Department of Natural Resources, 1986).

Goodyear (1985) investigated the effects of pollution-related mortality on Maryland striped bass, but found it was currently impossible to determine the relative contribution of fishing mortality and contaminant mortality. Contaminants were found in all life-history stages of striped bass in Maryland waters, however, no single contaminant was implicated in the decline. The same situation occurs with the striped bass in San Francisco Bay Delta, although fishing mortality is thought to be less important than natural mortality (Stevens *et al.*, 1985). Population modelling of Chesapeake Bay stocks of striped bass by Goodyear (1985) suggested that an immediate reduction in fishing mortality would be beneficial regardless of the causal factors in the decline.

Storm run-off may also adversely affect San Francisco Bay populations of striped bass. The Mediterranean climate in the San Francisco Bay area, with hot dry summers, followed by heavy rainstorms, tends to increase the importance of storm run-off containing high levels of pollutants such as petrochemicals.

Both Chesapeake and San Francisco Bay Delta estuaries are adjacent to agricultural development. The San Francisco Bay Delta, is the drainage system for one of the most intensive agricultural areas in the world, the Central Valley of California, with very heavy usage of pesticides and herbicides of immense diversity.

Striped bass from estuarine populations occur in an environment with highly variable conditions of flow and with urbanization and attendant pollutant and water quality problems. Larval survival and population production is also highly variable. The persistence of many estuarine populations appears dependent on dominant year classes (e.g., 1970 in the Chesapeake System and 1965–66 in the San Francisco Bay population). It is possible that the intensifying instability of climate and resultant fresh-water flow, with increasing pollution is suppressing the survival of large year classes, thereby diminishing their influence on population persistence in the estuary. The life history adaptive capacities of both Chesapeake and San Francisco Bay populations of striped bass may be increasingly unable to keep pace with their rapidly changing and deteriorating habitats.

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Cooperative Fisheries Oceanography Cruise

■ Scientists from the Southwest Fisheries Center Honolulu Laboratory of the National Marine Fisheries Service (NMFS) recently returned from a 30-day cruise collecting biological and oceanographic information from waters over and surrounding the central North Pacific seamounts.

Specifically, research operations were conducted aboard the National Oceanic and Atmospheric Administration ship *TOWNSEND CROMWELL* at Southeast Hancock Seamount, which is located about 200 nautical miles northwest of the Hawaiian Archipelago and just within the U.S. 200-mile Exclusive Economic Zone (EEZ).

"From a historical standpoint, the results would hopefully provide valuable insight into what once was a viable commercial fishery for Soviet and Japanese fishing ventures," said Richard S. Shomura, director of the NMFS Honolulu Laboratory. Shomura added that the seamounts provided habitat for large concentrations of fish, in particular the target species of fish known as the pelagic armorhead. In the spring of 1985, when catches of armorhead were nearly exhausted by the fishing pressure applied by foreign vessels, the NMFS closed the seamounts within the EEZ to all foreign fishing. The Honolulu Laboratory has since continued to monitor and explore the dynamics associated with abrupt topographical features such as the seamounts present. Chief scientist Michael P. Seki reported that fishery operations on the cruise involved primarily bottom longlines and bottom trawling gear. Collection of oceanographic data involved sampling along predetermined transects with such equipment as an acoustic Doppler current profiler, a geomagnetic electrokinetograph, hydroacoustic echo sounders, various small nets and water bottles.

In addition to Seki, scientific personnel on the cruise were research assistants Russell Y. Ito, Frank A. Parrish, Dennis Therry, and Christopher D. Wilson. Also participating on the cruise were cooperating scientists Dr. Jed Hirota and James Finn from the University of Hawaii Department of Oceanography, and Dr. Peter Koske and Thorsten Knutz from Kiel University in the Federal Republic of Germany.

The *CROMWELL* is operated by the Pacific Marine Center, National Ocean Service, NOAA, and is attached to the Honolulu Laboratory. The Commanding Officer on the *CROMWELL* is LCDR Robert Pawlowski. . . . **Richard Shomura**

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MIGRATION PATTERNS OF TUNA IN THE PACIFIC

Dr. Richard S. Shomura

Dr. Richard Shomura has served as Director of the Honolulu Laboratory of the National Marine Fisheries Service (NMFS) since 1973. Previously, he was Director of the NMFS Tiburon Fisheries Laboratory in California. Dr. Shomura is a past president of the Hawaii chapter of the American Fisheries Society. He received his M.S. in Zoology from the University of Hawaii in 1961.

* * *

(EXCERPTS FROM SLIDE PRESENTATION)

The recent extension of coastal jurisdiction out to 200-miles by the Pacific Basin countries has resulted in dramatic changes in fisheries strategies, fisheries policies, and international law. I do not plan to go into details of the high-seas tuna fisheries or the interaction of the high-seas fisheries with coastal fisheries and how these relate to the changes in coastal jurisdiction. With the brief time available, I will provide an overview of the movement patterns of several commercially important tuna species in the Pacific.

I should note that the tuna have been one of the key issues in international fisheries management and have been the cause of many legal problems as they relate to pelagic resources. The U.S.A. considers the tuna as highly migratory and, thus, does not include them in the MFCMA. While this interpretation is held by the U.S.A., other countries do not hold similar views. Instead, they view the tuna resources as being under their jurisdiction within the internationally accepted 200-mile zone. Since movement patterns are germane to the tuna issue, I will provide some information on the distribution and movements of several selected species of tunas and billfishes.

Tunas are related to the bonitos, mackerels, and are distantly related to billfishes. Based on the most recent FAO statistics for 1985, the world nominal catch was estimated to be nearly 85 million metric tons. Of the 85 million metric tons, the catch of tunas, bonitos, and billfishes was estimated to be 3.2 million metric tons, or roughly 3.8% of the total world landings. As you are aware, the tunas represent a high economically valued resource to many nations, especially to the Pacific island nations.

In looking at the distribution of the tunas across the world's oceans, the Pacific is by far the largest producer of tunas. In 1985, the Pacific produced 64% of the commercially important species. When I say commercially important I am including the albacore (Thunnus alalunga), northern bluefin tuna (T. thynnus), southern bluefin tuna (T. maccoyii), bigeye tuna (T. obesus), yellowfin tuna (T. albacares), and skipjack tuna (Katsuwonus pelamis). I should note that there are several other species that, although not commercially important, are very important to the artisanal fisheries that occur throughout the world, especially in the island areas of the world's oceans.

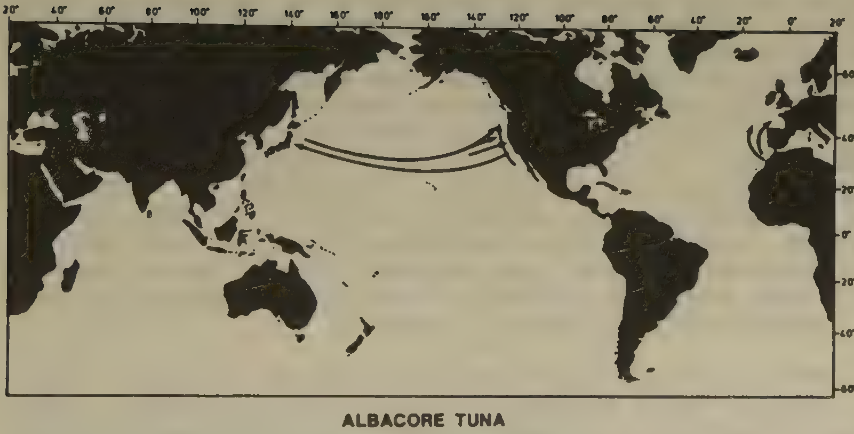
The skipjack and yellowfin tunas are the most important of the commercially caught tunas. The world catch of skipjack tuna in 1985 was 892,200 metric tons, of which 637,000 metric tons were taken from the Pacific. The bulk of skipjack tuna was taken in the central and western Pacific, mostly as a result of the newly established purse seine fisheries in the region. The yellowfin catch is also important in the Pacific. Of the world catch of 740,000 metric tons, the Pacific landed 470,600 metric tons or roughly 64%.

Migration Patterns

The distribution of albacore ranges from 40 degrees north latitude to 40 degrees south latitude. This species is taken by several types of fishing gear including troll, pole and line, and longline. In terms of movement patterns, Figure 1 illustrates some of the results based on tag release and recovery data. Most of the tagging has been done in the North Pacific. Although we do not have definitive data on the stock structure of the albacore in the Pacific, the distributional and spawning data suggest two separate stocks: one in the North Pacific and one in the South Pacific.

In terms of movement, one can describe the albacore as highly migratory because it undergoes extensive trans-Pacific movements; at least, this would describe the North Pacific stock. Not much is known of the South Pacific albacore because tagging has only recently been initiated for this resource in the South Pacific. To date, we have recovered only one tagged albacore from several thousand releases.

The bluefin tunas also show extensive trans-ocean movements. It should be noted, however, that these tuna species as well as a number of other tuna species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ALBACORE TUNA

Figure 1. Movement patterns of albacore tuna in the Pacific, as determined from capture and release studies. Arrows and terminuses indicate points of release and capture, respectively. Data are from Joseph et al (1979).

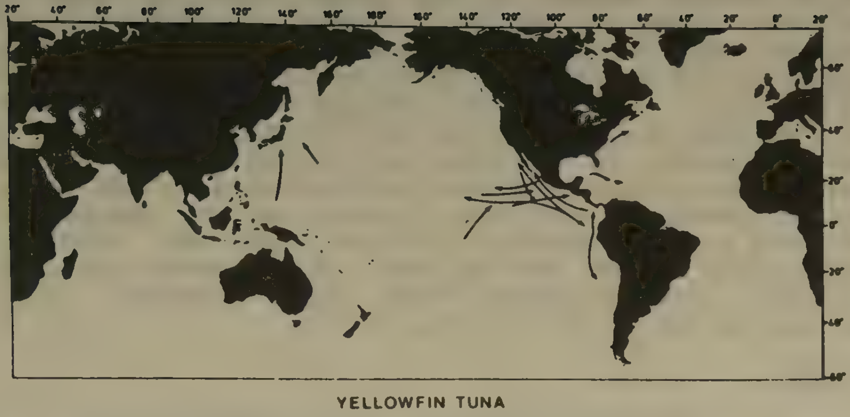
also are caught in large numbers close to shore. The northern bluefin tuna has been traditionally taken by traps in coastal waters of Japan. Because of their extensive movements, the bluefin tunas can be considered "highly migratory". In analyzing movement patterns based on tag release and recovery data, it should be noted that fishing effort is not uniformly distributed; thus, interpretation of the data may be biased by differences in fishing effort. Where we see tag recoveries, it may simply reflect more intensive fishing effort in that region.

The yellowfin tuna is found in tropical waters worldwide. This species is taken by a number of different types of gear. Recreational fishermen catch this species with troll gear, while commercial fishermen use a wide variety of fishing gear to capture this species. Commercial fishermen use troll, pole and line, handline, longline, and purse seine gears. The movements of yellowfin tuna are shown in Figure 2. Unlike the other tuna species that I have described thus far, the yellowfin tuna does not appear to move extensively, at least not as much as the albacore or bluefin tunas. Of the tens of thousands of yellowfin tuna tagged in the eastern Pacific by the Inter-American Tropical Tuna Commission (IATTC), nearly all were recovered in the same general area. These appears to be some movement of the yellowfin tuna offshore from the eastern part of Central America.

The skipjack tuna is also caught by several types of fishing gear including troll, pole and line, and purse seine. In recent years, there has been a considerable amount of tagging of this species. In the late 1970's the South Pacific Commission (SPC) tagged about 150,000 skipjack tunas from throughout the central and western Pacific. Figure 3 presents some of the results of this tagging study. There appears to be extensive movements by the skipjack tuna. To date, SPC scientists have not been able to discern any patterns that would suggest the existence of independent stocks of skipjack in the western Pacific. As with other tuna species, the skipjack tuna is found in waters close to shore as well as in waters considerable distances from shore; the skipjack tuna has been caught as far as 40 north latitude in the North Pacific.

Among the other commercially important tunas, the bigeye tuna also shows extensive movements. The tag release and recovery data for bigeye tuna show patterns similar to that of albacore.

Although billfishes are not the subject of this presentation, it may be instructive to note some of the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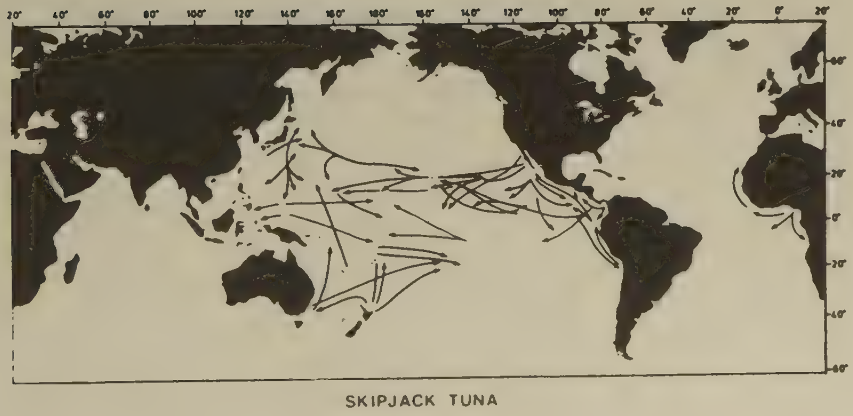
YELLOWFIN TUNA

Figure 2. Movement patterns of yellowfin tuna in the Pacific, as determined from capture and release studies. Arrows and terminuses indicate points of release and capture, respectively.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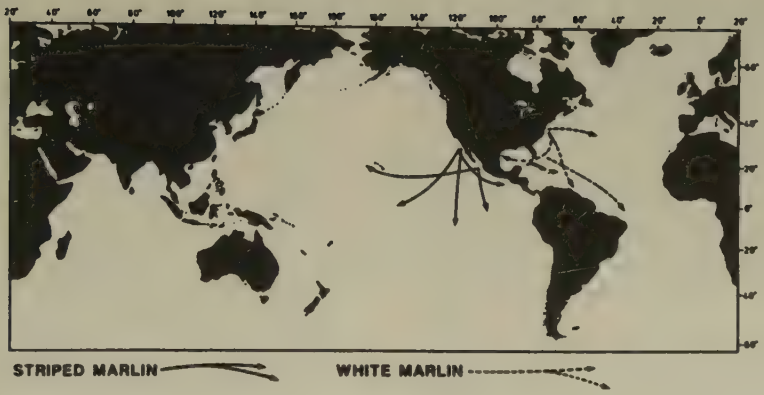
SKIPJACK TUNA

Figure 3. Movement patterns of skipjack tuna in the Pacific, as determined from capture and release studies. Arrows and terminuses indicate points of release and capture, respectively. Data are from Joseph et al (1979).

extensive movements undertaken by some billfish species --instructive because, unlike tunas, the billfishes are included under the MFCMA. Figure 4 shows the tag release and recovery of striped marlin (Tetrapturus audax) in the Pacific and white marlin (T. albidus) in the Atlantic. Some of the striped marlin show extensive movements; one striped marlin tagged off Mexico was recovered in the Hawaiian Islands area. A more remarkable movement has been demonstrated by the black marlin (Makaira indica). A black marlin tagged off Cape San Lucas in Mexico in January 1983 was recovered off Norfolk Island, New Zealand, in September 1984. By straight line distance, this fish traveled 5,760 nautical miles over a 613-day period.

SUMMARY

We do not fully understand the stock structure and movement patterns of the various species of tunas and billfishes. There appears to be ample evidence that some species of tunas move extensively; these species would include the albacore, northern bluefin tuna, southern bluefin tuna, bigeye tuna, and skipjack tuna. The yellowfin tuna does not appear to move as extensively. Although data are limited, some species of billfish appear to move extensively also.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STRIPED MARLIN
WHITE MARLIN

Figure 4. Movement patterns of striped marlin in the Pacific and white marlin in the Atlantic, as determined from capture and release studies. Arrows and terminuses indicate points of release and capture, respectively. Data are from Joseph et al (1979).

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CALCOFI TIME SERIES: AN OVERVIEW OF FISHES

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POPULATION PROCESSES

The stated objective of CalCOFI is "to determine what controls variations in population size and availability in oceanic fishes off the west coast of North America." The chief disciplines to be applied to this work are fishery biology—the study of population and biological community reactions to commercial harvest—and biological oceanography—the study of how the biological and physical environment affects biological populations and communities.

Murphy (1966, p. 69) concluded that the Pacific sardine was overfished and that the virtually unfished anchovy had increased to fill its niche as a regionally dominant planktivore. However, the fossil-scale record (Soutar and Isaacs 1974), which is considered to be a useful index of population size and availability, shows that precipitous declines in the Pacific sardine population between 1930 and 1960 off southern California were exceeded between 1850 and 1870, when there was no fishery, and between 1900 and 1915, when the fishery was small.

Smith (1972) reviewed the time series of sardines and anchovies as indexed by their larvae and concluded (p. 873) that the size-frequency curves of the larvae of the two species were so invariant among years that competition between the two species, if any, would most likely occur at the juvenile and prerecruit stages of either species. This was contrary to the argument of Isaacs (1965) that the recruitment of anchovy and sardine could be projected from day/night differences in the early larval stages. Smith (1972) also recommended that the ideas should be tested with surveys of larger larvae and juveniles. He pointed out that the number of batches of spawn per unit time might be plastic (Smith 1972, p. 873). This biases the indices of population size by failing to estimate the degree of interannual variation in the amount of spawning per unit time per unit of adult biomass. In this connection it was pointed out that the decline of sardine spawning in the spring and summer has coincided with an increase of spawning in spring by the anchovy. Current estimates of historical biomass (Lo 1985) indicate that apparent increase in anchovy spawning biomass following the collapse of the sardine population could result from increased repetitive spawning as well as increased anchovy spawning biomass.

Another element in variations in population size and availability of fishes is the biological community structure. Moser et al. (1987) showed that there were major changes in mesopelagic and epipelagic fish recurrent groups during climatic changes. But data from only seven years centered on the 1957 El Niño were analyzed, so the long-term coherence of the changes cannot yet be assessed. For the same period, Colebrook (1977) showed that there were major shifts in the types of zooplankton, with particularly significant shifts in the north-south distribution of zooplankton and secondary changes in the onshore-offshore abundance.

What are the critical time and space scales for understanding the fluctuations in abundance of oceanic fishes off the North American Pacific coast? Haury et al. (1978) suggest a rationale and design:

> Since the study of the causes of variation in population size is one of the chief objectives in ecological research, one reasonable approach is to select for study those scales where the variation seems to be the greatest . . . . the [length scale between] . . . 50 and 1000 km and the [time scale of] . . . one half to 80 years is such a scale. This scale is remarkably similar to the one of Stommel's [time and space variation diagram] showing the most "energetic" part of the ocean. Further, it is about the size of many populations or stocks of planktivorous fish. This may not be purely coincidental.

While the Murphy (1966) proposal that the northern anchovy biomass has replaced the sardine cannot be supported by current biomass estimates of the period he studied (1932–65) or the longer period of scale-deposition rates (Soutar and Isaacs 1974), he did demonstrate an interesting coherence in spawning success rate lasting 3–5 years (Murphy 1966, p. 53). Simple population theory would suggest that a population at the carrying capacity of the environment would have an alternation of spawning success rates, and that populations over

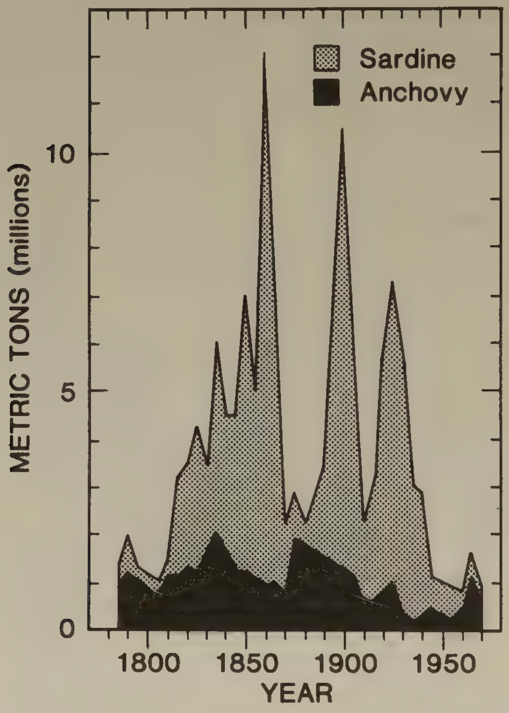

Figure 1. Revised estimate of the spawning biomass of northern anchovy between 1790 and 1970 (180 years at 5-year intervals) derived from the scale-deposition rate in two anoxic basins (Soutar and Isaacs 1974) and adjusted to the spawning biomass determined between 1980 and 1985 for northern anchovy (Methot and Lo 1987), and estimated between 1951 and 1969 (Lo 1985). The Pacific sardine biomass remains the same as in Smith 1978.

the carrying capacity would have poor spawning success. Murphy described multiyear sets of spawning success or failure as indicating population growth mediated by changes in the carrying capacity rather than as a population equilibrium about a fixed carrying capacity. In addition to the 3–5-year coherence in spawning success, there appear to be long-term trends in the sardine and anchovy populations in the scale-deposition record of Soutar and Isaacs (1974) (Figure 1).

It is the purpose of this paper to speculate on the future directions of CalCOFI field work as it relates to processes and patterns that control the variations in population size and availability of oceanic fishes. Many new opportunities are afforded by the technical advances of the last 50 years. The precision and accuracy of primary production estimates have grown steadily. Lasker (1970) specified the level of production necessary for maintaining the Pacific sardine population. The population dynamics and energetics of several other important herbivorous and omnivorous species in the area have been elaborated. The key ecosystem boundaries, and the fauna and their temporal shifts have been described. The scientific basis for conducting ecosystem management exists for some groups of species, but there are formidable technical problems in implementing management.

How Do Population Parameters Vary in Northern Anchovy?

Population maintenance includes the processes of growth, survival, and reproduction. There is important new work on these processes for the massive local population of northern anchovy. Hunter and Leong (1981) found that northern anchovy females spawned 20 batches per year. The energy for only 2 batches was resident in the ovaries; about 13 could be formed from stored fat; the rest would therefore have to be derived from local contemporaneous primary and secondary plankton production. Smith and Eppley (1982) found that the abundance of anchovy larvae in the Southern California Bight region was positively associated with zooplankton standing stock in the previous summer and with primary production in the same quarter.

Theoretically, it is possible to specify all the variations in the northern anchovy population by knowing the variations of reproductive effort of the adults, and growth and survival of all stages (Smith 1985a). Current methods of estimating reproductive effort in anchovy do not depend on index correlations, but directly estimate the reproductive parameters (Lasker 1985, Introduction) and also allow the estimation of embryonic and larval survival. The short 6-year period for which this has been done is not adequate for time-series analysis, but it may be interesting to compare the variations in reproductive and early life-history parameters with the actual variation in spawning biomass. This 6-year period includes 2 years before and after the 1982–1983 El Niño (Chelton et al. 1982; Smith 1985b; Fiedler et al. 1986).

One can see from Table 1 that there are many variables in the reproductive process which may be responsible for a considerable fraction of the recruitment variability. In this 6-year period, the absolute recruitment in numbers of fish varied 64%. The relative recruitment rate in terms of number of recruits per ton of spawners varied 104%. The reproduction parameters varied from a low of 14%

TABLE 1
Interannual Variation of Population Parameters of the Northern Anchovy (*Engraulis mordax*), 1980–85

Parameter	Mean	Standard deviation	Interannual coefficient of variation	Ref.*
Spawning biomass (thousand metric tons)	567	198	35%	1-6
Spawning area (naut. sq. mi.)	25,167	7,679	31%	1-6
Density (grams per sq. m.)	7	3.3	47%	1-6
Spawning female wt (grams)	14.5	3.1	21%	1-6
Specific fecundity (eggs per gram per batch)	513	71.7	14%	1-6
Batch fecundity (eggs per batch)	7,476	2,079	28%	1-6
Interval (days between batches)	8	1.7	21%	1-6
Mean age (years on Feb. 1)	1.8	0.4	23%	8
Year class (10^9 fish)	51	33	64%	8
Juvenile length (mm on Oct 1)	82	7.6	9%	7
Egg production (10^{12} eggs/day)	18	5	28%	1-6
Egg mortality (daily instantaneous)	0.24	0.09	38%	1-6
Yolksac mortality (daily instantaneous)	0.08	0.018	22%	7
Firstfeed mortality (daily instantaneous)	0.14	0.019	14%	7
2-8 mm mortality	1.7	0.36	21%	7
8 mm larvae production (10^{12}/day)	0.19	0.05	27%	7
Eggs to 8 mm (eggs per 8 mm)	102	35	34%	Derived from 7
Year class (thousand fish per MT of spawner)	116	121	104%	Derived from 7

*References:
1. Bindman 1986; 2. Hewitt 1985; 3. Picquelle and Hewitt 1984; 4. Picquelle and Hewitt 1983; 5. Stauffer and Charter 1982; 6. Stauffer and Picquelle 1981; 7. Fiedler et al. 1986; 8. Methot 1986.

for specific fecundity and first-feeding mortality to about 30% for egg mortality, egg production, and batch fecundity. We have not considered any environmental factors, but these internal population factors seem large enough so that combining them with unlisted factors could well account for the observed recruitment variation.

What is missing is a data set designed to partition the relative importance of controls on recruitment. In particular, it remains to be seen how the strong environmental controls interact with the weak population size controls and where in the life cycle these interactions take place. Early life stages can occasionally form part of the variation in recruitment, but much expanded work must be done to sample late larvae and juveniles in addition to (not instead of) early larvae and embryos.

The major problems in sampling late larvae and juveniles (which have been largely solved for embryos and early larvae) are: (1) they are widespread geographically, and there is no way to detect which larvae or juveniles will eventually contribute to recruitment; (2) the late larvae and juveniles are extremely mobile and in schooled patches, thus more sophisticated samplers and more numerous samples will be needed to determine abundance of these stages; and (3) their growth rate is much more plastic than embryos and early larvae, so that regional and seasonal differences in growth rate will require many age and size determinations. In short, analysis of these late larval and juvenile stages will not add to the understanding of the entire life cycle until more money, ship time, and personnel are available for their study. Obviously, as Peterman et al. (1988) point out, the prediction of recruitment could improve as the time between the prediction and recruitment is shortened; this will come about only as it becomes economically feasible.

Another deficiency of all analyses of recruitment variability to date is the inability to assemble the sources of variability that arise from other spatial elements and in other time periods. For example, in addition to being fished, the northern anchovy is preyed upon by a wide variety of fishes, birds, marine mammals (which migrate here from the tropics and from the Arctic, thousands of miles outside the anchovy habitat), and by temperate and tropical tunas (some of which are spawned in the western Pacific 6000 miles away). Some major predators on the anchovy at different stages have life cycles of the order of weeks or months; others have life cycles of years to decades. It would not be unusual, then, for population responses to additional predation pressure on sardines or anchovies to take a decade if the population undergoing change were the northern fur seal; years if predatory populations were Pacific mackerel or one of the mesopelagic fishes; or months if the predatory population were euphausiids or copepods.

Are Time Series of Populations off California Stochastic or Coherent on Long Time Scales?

In Table 2 we have listed measures of periodicity of the fossil-scale series of Soutar and Isaacs (1974). The technique was to count and identify the scales in 5-year intervals for 190 clearly marked varves. We analyzed the time series with an integrated periodogram to determine whether the

TABLE 2

Coherence of Successive Scale Deposition Rates

	5-yr periods	Frequency[a]	Significance[b]	Period[c]
Anchovy	38	low	>0.95	50 yr
Sardine	38	low	>0.95	40 yr
Pacific hake	38	low	>0.75	65 yr
Pacific mackerel	38	low	>0.75	50 yr
Pacific saury	38	low	>0.75	30 yr
Other scales	38	low	>0.95	50 yr

[a] Low frequency of change in trend equals high coherence.
[b] Significance of deviation from random in an integrated periodogram.
[c] Major period in a time series.

TABLE 3

Comparison of Cross-Correlation between the Scale-Deposition Time Series at the Santa Barbara Basin and the Soledad Basin (1000 km Southeast)

	Zero lag R	Min R	Lag	Max R	Lag
Northern anchovy	0.26	−0.28	5	0.43	−3
Pacific sardine	−0.02	−0.21	−3	0.24	1
Pacific hake	−0.17	−0.37	−4	0.50	5
Pacific mackerel	0.37	−0.15	−5	0.57	−1
Pacific saury	0.65	−0.09	2	0.66	−1
Other	0.03	−0.33	−5	0.18	1

series deviated from the random on the low-frequency or high-frequency side and to determine the significance of the cumulative deviation. Each time series was categorized as low-frequency if all periods were above white noise. If they were below the 0.75 probability line the time series was labeled < 0.75; if the series was between the 0.75 and 0.95 probability lines the time series was labeled < 0.95; and if the series projected above the 0.95 line the series was labeled > 0.95. The period was chosen from the maximum peak (10 sample units = 50 years) on the periodogram when there was more than one peak.

We can see from Table 2 that there is major agreement among the species as to the spectral composition of the time series. To varying degrees of significance, the spectrum is of low frequency. The period of change is long, ranging from 30 years in the Pacific saury to 65 years in the Pacific hake. One may assume that the mechanism is environmental, because the generation time of these species is always less than 10 years. In addition to the 3–5-year scale detected in spawning success of sardine (Murphy 1966), we must now be alert to mechanisms operating on a much longer scale. In particular, for management purposes we will need criteria for determining changes in regime from periods of successful reproduction to unsuccessful reproduction.

How Do the Time Series of the Species Compare from Two Collection Sites 1000 km Apart?

Soutar and Isaacs (1974) reported two time series, one from the Santa Barbara Basin at 34°N and one from the Soledad Basin at 26°N. We examined cross-correlations with lags from −5 to 5 representing a period of 55 years. In Table 3 we have the correlation coefficient at the 0 lag or contemporaneously. We have also listed the minimum and maximum cross-correlation coefficients with the lag at which this was achieved.

The Pacific saury, with a transpacific distribution, shows the most cross-correlation between these sites 1000 km apart. The Pacific sardine shows the least. One may conclude from this that the relationships between the sites are generally weak. This could be interpreted to mean that the tendency for these populations to range north and south with long-term changes in climate is nil and that population changes at one site are neither in phase nor out of phase with populations at the other site.

At a Scale-Deposition Site, Do Population Trends of the Major Species Show Interactions Affecting Population Abundance?

To what degree do these populations change at the two sites in response to one another? Table 4 for the Santa Barbara Basin scales and Table 5 for the Soledad Basin scales list the zero-lag correlation coefficients, the minimum cross-correlation coefficient and its lag, and the maximum cross-correlation coefficient and its lag. Here again, as in the species comparisons between basins, most of the correlation coefficients are low. This suggests that within the scale-deposition area of a basin the population densities of the species are unrelated. Some exceptions at the Santa Barbara Basin include the zero-lag (same 5-year period) correlation of 0.66 between the anchovy and hake populations. This means that 40% of the biomass series of either species is controlled by the other or by a common environmental factor. The correlation coefficient between Pacific mackerel and Pacific saury is 0.65 with a lag of 3 (15 years). The largest negative influence is between the northern anchovy and Pacific mackerel at −0.43 with a lag of −1. This suggests that a high biomass of Pacific mackerel is followed in the next 5-year period by a low biomass of anchovy; however, the control is low (about 20%).

At the Soledad Basin there appears to be a bit more structure among the species. Here the an-

TABLE 4
Cross-Correlation Coefficients among Several Species at the Santa Barbara Basin Site

	Pacific sardine	Pacific hake	Pacific mackerel	Pacific saury	Other
No lag					
Northern anchovy	0.33	0.66	−0.36	−0.38	0.03
Pacific sardine		0.38	−0.06	−0.26	−0.21
Pacific hake			−0.18	−0.24	0.01
Pacific mackerel				0.14	−0.11
Pacific saury					0.24
Minimum (lag)					
Northern anchovy	−0.02(−2)	−0.02(−5)	−0.43(−1)	−0.45(1)	−0.19(4)
Pacific sardine		−0.29(4)	−0.35(−4)	−0.31(−2)	−0.29(−2)
Pacific hake			−0.36(−5)	−0.34(−1)	−0.40(4)
Pacific mackerel				−0.19(−3)	−0.33(−4)
Pacific saury					−0.21(−4)
Maximum (lag)					
Northern anchovy	0.41(4)	0.66(0)	0.17(2)	0.04(5)	0.36(−5)
Pacific sardine		0.46(−1)	0.14(2)	0.13(5)	0.18(4)
Pacific hake			0.25(5)	−0.01(−5)	0.53(−4)
Pacific mackerel				0.65(3)	0.18(1)
Pacific saury					0.24(0)

Analysis of data from Soutar and Isaacs 1974.

chovy and hake are negatively correlated at all lags. The correlation is most negative at −1 lag ($r = -0.50$), and it is generally the same at zero lag (−0.45). Sardines are positively correlated with Pacific mackerel ($r = 0.68$, lag 2) and Pacific saury ($r = 0.79$, lag 3). Pacific mackerel is also positively correlated with Pacific saury ($r = 0.64$, lag 1). Anchovy is positively correlated at all lags with the category "other" scales, with a maximum correlation of 0.81 at 0 lag. Hake is also correlated negatively ($r = -0.56$) with "other" scales at a lag of −2 in the Soledad Basin area.

From this analysis, it appears that controls of fish populations on each other are weak, and common responses to environmental changes are similarly weak. Thus although Murphy (1966), Lasker (1970), and Smith and Eppley (1982) all agree that the major pelagic schooling stock, either sardine

TABLE 5
Cross-Correlation Coefficients among Several Species at the Soledad Basin Site

	Pacific sardine	Pacific hake	Pacific mackerel	Pacific saury	Other
No lag					
Northern anchovy	−0.26	−0.45	−0.19	−0.29	0.81
Pacific sardine		0.24	0.38	−0.10	−0.22
Pacific hake			0.44	0.33	−0.22
Pacific mackerel				0.31	−0.19
Pacific saury					−0.17
Minimum (lag)					
Northern anchovy	−0.33(−5)	−0.50(−1)	−0.35(−3)	−0.34(3)	0.11(5)
Pacific sardine		−0.24(−5)	−0.25(−5)	−0.21(−4)	−0.33(−4)
Pacific hake			−0.11(−3)	−0.18(−5)	−0.56(−2)
Pacific mackerel				−0.15(−4)	−0.35(3)
Pacific saury					−0.31(−3)
Maximum (lag)					
Northern anchovy	−0.13(−2)	−0.17(5)	−0.18(1)	0.00(−5)	0.81(0)
Pacific sardine		0.46(−2)	0.68(2)	0.79(3)	−0.12(−2)
Pacific hake			0.44(0)	0.47(1)	−0.06(5)
Pacific mackerel				0.64(1)	−0.06(5)
Pacific saury					−0.01(4)

Analysis of data from Soutar and Isaacs 1974.

or anchovy, is a massive consumer of production relative to the total produced in the California Current system, there does not seem to be any evidence from the fossil-scale record that they compete within a habitat or migrate from one end of the habitat to another. Competition, if any, must be part of a vast and changing array of as yet unmeasured population controls on the major species. It seems possible that abundant mesopelagic populations which migrate to the epipelagic zone and are piscivorous and planktivorous could exert predatory control on the larvae and juveniles of the common epipelagic fishes.

COMMUNITY PROCESSES

The work of Scofield (1934) revealed that the sardine spawned throughout a large proportion of the California Current region, and this was confirmed by Ahlstrom (1948) during the beginnings of the CalCOFI program. Thus a plankton survey designed to comprehensively sample sardine spawning had the potential to yield biogeographic information on a large array of marine organisms. This potential was realized only through the research efforts of dedicated scientists.

Dr. Elbert Ahlstrom was in charge of ichthyoplankton, and from the beginning was determined to identify each sample as far as his knowledge would allow. This knowledge grew rapidly; he soon became preeminent among the small group of people working on ichthyoplankton around the world. Thus, while the primary focus was on the early life history of the sardine and later its relation to the anchovy (Ahlstrom 1966), he was steadily building a fund of information on the ontogeny, systematics, and biogeography of eastern Pacific fishes. His series of definitive papers on early life history and his active role in training and guiding young researchers were principal factors in building a once modest group of devotees into a major field of ocean science. His contributions to the ontogeny and systematics of fishes culminated in an international symposium and a book that summarized and integrated the existing knowledge of these fields (Moser et al. 1984).

The patterns of distribution and abundance of larvae of the principal fish taxa in the California Current and adjoining regions have been reported by Ahlstrom and his co-workers in the CalCOFI Atlas series (Ahlstrom 1969, 1972a; Ahlstrom and Moser 1975; Ahlstrom et al. 1978; Kramer 1970; Kramer and Ahlstrom 1968; Hewitt 1980) and in individual research papers (Ahlstrom 1961, 1965, 1971, 1972b; Ahlstrom and Ball 1954; Ahlstrom and Counts 1955, 1958; Ahlstrom and Stevens 1977; Ahlstrom et al. 1976; Ambrose et al. 1983; D'Vincent et al. 1980; Kramer 1960; Loeb et al. 1983a, b, c; Moser and Ahlstrom 1970; Moser et al. 1973, 1977, 1983, 1986; Stevens and Moser 1982; Sumida et al. 1979, 1985). Lack of a computer data base for CalCOFI has limited our ability to analyze the time series. Since 1983 (Charter et al. 1986[1]) we have been working to remedy this and in the near future will publish 23 ichthyoplankton data reports covering CalCOFI surveys from 1951 to 1981 (see Appendix); the computer data base will be made available to the public through the on-line system described by Roger Hewitt in this volume.

Concurrently with the development of the data base, we have begun to analyze the larval fish assemblages of the California Current region. The northern anchovy, *Engraulis mordax*, has increased in relative abundance throughout the three decades from 1951 to 1981 and accounts for about half the larvae collected over this span (Table 6). Next most numerous are three taxa that consistently rank 2d, 3d, or 4th through this time span: the Pacific hake (*Merluccius productus*), the eastern tropical Pacific gonostomatid *Vinciguerria lucetia*, and the rockfish genus *Sebastes*, which includes over 70 species in the survey area. These 4 top-ranking species represent 72% of all larvae taken. Next in overall rank are 3 midwater species: the deepsea smelt *Leuroglossus stilbius* and two mesopelagic lanternfish, *Triphoturus mexicanus* and *Stenobrachius leucopsarus*. Eighth in overall rank is the sanddab genus *Citharichthys*, which includes 6 species in the CalCOFI region. The remaining 2 species in the top 10 are the Pacific sardine (*Sardinops sagax*) and the jack mackerel (*Trachurus symmetricus*), both of which have shown a relative decline throughout the time series.

The faunal affinities of these top-ranking taxa reflect the transitional nature of the CalCOFI region. Congeners of the anchovy, sardine, jack mackerel, and hake are also abundant in the three other eastern boundary currents of the Pacific and Atlantic. *S. leucopsarus* is a subarctic-transitional species, and *L. stilbius* has a transitional distribution, *sensu* Johnson and Brinton (1965), extending northward from the California Current across the Pacific in a narrow zone between the subarctic and central water masses. *Sebastes* is a subarctic-tran-

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[1] Charter, R., D. A. Ambrose, H. G. Moser, E. M. Sandknop, P. E. Smith, E. G. Stevens and B. Y. Sumida. The CalCOFI ichthyoplankton data base and data reports. Poster presented at CalCOFI Annual Conference, Lake Arrowhead, California, October 21–23, 1986.

TABLE 6

Relative Abundance of the 10 Top-Ranking Larval Fish Taxa Taken on CalCOFI Cruises, Shown as Standardized Counts Pooled for Each Decade

Taxon	1951–81			1951–59			1960–69			1972–78			1980–81		
	Rank	Count	Percent	Rank	Count	Percent	Rank	Count	Percent	Rank	Count	Percent	Rank	Count	Percent
Engraulis mordax	1	5,645,276	49.0	1	1,195,566	33.0	1	2,473,787	54.0	1	1,491,654	57.7	1	484,269	65.5
Merluccius productus	2	1,014,627	8.8	2	523,588	14.4	3	268,044	5.9	2	204,259	7.9	5	18,736	2.5
Vinciguerria lucetia	3	905,814	7.9	3	335,862	9.3	2	384,025	8.4	4	149,191	5.8	3	36,736	5.0
Sebastes spp.	4	718,841	6.2	4	251,065	6.9	4	259,938	5.7	3	157,430	6.1	2	50,408	6.8
Leuroglossus stilbius	5	444,399	3.9	5	176,671	4.9	6	165,733	3.6	5	76,312	3.0	4	25,683	3.5
Triphoturus mexicanus	6	396,178	3.4	6	165,238	4.6	5	170,755	3.7	8	47,799	1.8	7	12,386	1.7
Stenobrachius leucopsarus	7	313,131	2.7	8	132,683	3.7	7	104,316	2.3	6	60,492	2.3	6	15,640	2.1
Citharichthys spp.	8	275,176	2.4	9	128,342	3.5	8	81,621	1.8	7	56,498	2.2	8	8,715	1.2
Sardinops sagax	9	218,722	1.9	7	136,883	3.8	10	62,845	1.4	16	12,946	0.5	13	6,048	0.8
Trachurus symmetricus	10	206,235	1.8	10	116,148	3.2	9	69,959	1.5	14	16,115	0.6	14	4,013	0.5
			87.9			87.3			88.3			87.9			89.6
All taxa		11,532,013			3,628,396			4,578,555			2,586,250			738,812	
No. stations		30,296			14,025			11,256			4,037			978	

sitional shorefish group, and the various species of *Citharichthys* are found in coastal waters from the subarctic through the tropics. *T. mexicanus* is a subtropical species abundant in the southern reaches of the California Current, and *V. lucetia* is an eastern tropical Pacific species. Central water mass species are not abundant in the CalCOFI samples; however, warm-water cosmopolites such as the myctophids *Diogenichthys atlanticus*, *Hygophum reinhardtii*, and *Myctophum nitidulum* appear where central water impinges on the California Current off southern California and Baja California. The distributional patterns of the principal and less-abundant larval fish taxa in the CalCOFI region are closely tied to water masses, clearly affirming what has been shown for a wide array of zooplankton species (Reid et al. 1978).

As a first step in studying potential environmental effects and species interactions, we performed a recurrent group analysis on the 7-year span of the time series from 1954 to 1960 (Moser et al. 1987). This period was chosen because there was maximum areal and seasonal sampling coverage during a sequence of anomalously cold and warm oceanographic regimes. Also, initial identifications of the samples were fairly reliable, and these were improved during the editing and verification of the data base. The recurrent group method identifies groups of taxa that occur together frequently and are consistently part of each other's environment. This method tends to avoid potential misinterpretations that can arise from abundance analyses of patchy organisms.

Analysis of nearly 200 taxa from the composite 7-year data set produced 9 recurrent groups formed by 30 taxa. Intergroup affinities produced two large complexes of 4 recurrent groups each. We refer to these as the "northern" and "southern" complexes, since their constituents had primarily warm- or cold-water taxa or were linked to warm- or cold-water taxa through affinity indices. Spawning was seasonal in most species, with winter or spring maxima in the northern complex and spring or summer maxima in the southern complex. Each complex consisted of a 5-member group with strong connections to the smaller groups in the complex.

The large group in the northern complex was a mix of abundant subarctic-transitional (*L. stilbius*, *S. leucopsarus*, *Sebastes* spp.) and transitional (*M. productus*, *Bathylagus ochotensis*) taxa, which were strongly interlinked with *E. mordax* and *S. sagax* in two other groups. In contrast to the northern and coastal nature of this complex, the southern complex comprised primarily mesopelagic species that inhabit more southerly and offshore waters. The 5-member group included transitional species (*Bathylagus wesethi*, *Lampanyctus ritteri*, *Symbolophorus californiensis*) and warm-water cosmopolites (*Cyclothone* spp., *Diogenichthys atlanticus*) that were strongly linked to an eastern tropical Pacific group (*V. lucetia*, *Diogenichthys laternatus*, *Hygophum atratum*, *Gonichthys tenuiculus*) and a group comprising transitional (*Trachurus symmetricus*, *Protomyctophum crockeri*) and subtropical (*T. mexicanus*) species. A third complex was associated with the extensive coastal shelf region of central Baja California and consisted of a group of four subtropical shorefish taxa.

The structure and composition of the groups varied in analyses of individual years, more so in the southern complex; however, the northern and southern complexes were generally conserved. The two complexes were linked by a single pairing

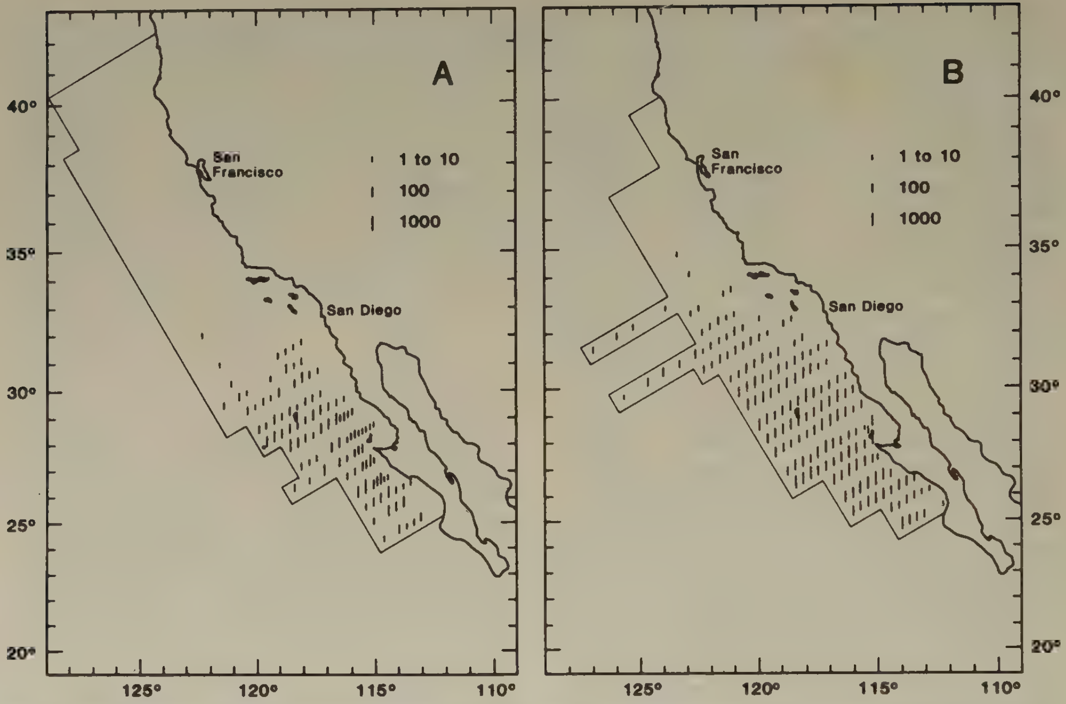

Figure 2. Change in distribution of larvae of *Vinciguerria lucetia* during cold (*A*) and warm (*B*) temperature regimes in the California Current region. Pooled numbers of larvae for three cold years (1954–56) and three warm years (1958–60) are indicated by exponentially scaled bars. The survey pattern for each series of years is outlined.

(*E. mordax-T. mexicanus*) in the composite analysis, although in some years the links between the two complexes were stronger and more numerous, and there was some switching of group members between complexes. Where this occurred, the southern complex group of *T. mexicanus-P. crockeri-T. symmetricus* and the northern complex group of *E. mordax-Citharichthys* were usually involved, emphasizing the transitional position of these taxa in the CalCOFI region.

Variation in the structure and composition of the complexes and their constituent groups was, in part, related to the major oceanographic changes that occurred during 1954–1960. Conditions in the first half of the 1950s were generally cool, culminating in the strong negative temperature anomaly during 1956. A warming trend began in 1957, leading to a major El Niño event in 1958 and 1959. Mixed-layer isotherms were shifted northward more than 200 km, shifting the distribution and abundance of some larval fish taxa northward, (Figure 2) and causing the above-mentioned changes in recurrent groups. These changes were not as great as those associated with the anomalously cold year of 1956, when affinity indices were lowered among southern complex species, and recurrent groups in this complex were markedly depauperate (see Moser et al. 1987 for details).

From this brief summary it is clear that the CalCOFI surveys reveal the major faunal associations and broadscale environmental interactions in the California Current region. This was particularly true for the 1950s, when monthly sample coverage extended over the full length of the pattern. Biogeographic information has diminished since 1960, with the areal and temporal shrinkage of the survey pattern; however, even the present minimal quarterly coverage of the Southern California Bight is sensitive to changes in ocean regimes because subtropical, eastern tropical Pacific, and central water mass species expand their spawning boundaries into this region. The original extensive coverage was also essential in defining the broad spawning ranges of commercial species such as Pacific hake, jack mackerel, Pacific mackerel, and the rockfishes. Fishery scientists have relied heavily on CalCOFI data in developing the knowledge required to manage these populations.

The early surveys also showed that many important coastal recreational and commercial species spawn off Baja California. Ocean whitefish (*Caulolatilis princeps*) appears to spawn exclusively off Baja California, since larvae have not been taken north of the Mexican border (Moser et al. 1986). White seabass (*Atractoscion nobilis*), yellowtail (*Seriola lalandi*), and bonito (*Sarda chiliensis*) spawn primarily off Baja California, with small numbers of larvae appearing off southern California (Moser et al. 1983; Sumida et al. 1985; original data). Barracuda (*Sphyraena argentea*) and California halibut (*Paralichthys californicus*) spawn off southern California, but the greater part of their spawning range extends the entire length of Baja California (Kramer and Smith 1973). Recruitment of these transboundary stocks to southern California is either dependent on or strongly influenced by stocks off Mexico. The United States and Mexico are highly interdependent in the use and management of these stocks, and if CalCOFI is to be involved in studies of their production and recruitment, the present survey pattern will have to be expanded south of the Southern California Bight.

During the past ten years there has been increased ichthyoplankton research on shorefish populations, primarily because of potential impacts of power plants and urban development (Brewer et al. 1981; Gruber et al. 1982; Schlotterbeck and Connally 1982; Barnett et al. 1984; Lavenberg et al. 1986; Walker et al. 1987). These workers have used CalCOFI ichthyoplankton techniques to study the zone between the most shoreward CalCOFI stations and the beach. One of their key findings is a distinct nearshore ichthyoplankton fauna, which peaks at about 40 – m bottom depth and is poorly sampled at the most shoreward CalCOFI stations. Many of these species settle to the bottom at early larval stages, apparently as an adaptation to remain nearshore, and there is a general tendency in these larvae to move downward and shoreward ontogenetically. Some species are neustonic and may be transported shoreward in surface slicks associated with tidally forced internal waves (Shanks 1983). Larvae of the nearshore assemblage are comparatively rare in CalCOFI samples, generally occur well seaward of their zone of settlement, and may represent reproductive wastage rather than potential recruits. Alternatively, they may possess behavioral mechanisms that allow far-ranging planktonic stages to recruit to the nearshore habitats of the adults. This question can be addressed by analyzing the CalCOFI and nearshore ichthyoplankton data bases that are presently being assembled, but it probably cannot be answered without concentrated field surveys in the transition region between the two zones.

An initial objective of the CalCOFI program was to determine the environmental and biotic factors that affect production, recruitment, and population fluctuations of the sardine. During the past 40 years the program has provided spawning biomass indices of the sardine, anchovy, and mackerels (Ahlstrom 1966; Smith 1972; Parrish and MacCall 1978; MacCall and Stauffer 1983) and has documented the continued decline of the sardine and concomitant increase of anchovy in the CalCOFI region. A recent modification of CalCOFI sampling design has allowed direct estimation of anchovy and sardine spawning biomass (Lasker 1985; Wolf et al. 1987). CalCOFI has been the foundation for a number of hypotheses: sardine-anchovy competitive exclusion (Murphy 1966; Ahlstrom 1967; Isaacs 1965); ocean transport-larval survival (Parrish et al. 1981; Simpson 1987); Lasker's (1975) stable ocean-larval survival hypothesis; and MacCall's density-dependent habitat selection model (MacCall 1980; Lasker and MacCall 1983). Correlation techniques support Lasker's hypothesis that wind-driven turbulent mixing increases mortality of early-stage anchovy larvae by dissipating food patches (Peterman and Bradford 1987) but do not support the hypothesis (Lasker 1981) that recruitment and year-class strength are determined by mortality of early-stage larvae (Peterman et al. 1988). The latter authors suggested that recruitment variability would depend on survival during the late larval-prerecruit stages, which are virtually absent from CalCOFI samples.

Our research on interannual variation of incidence and abundance of CalCOFI ichthyoplankton (Moser et al. 1987) suggests that a multispecies approach might provide recruitment information on species such as sardine and anchovy. These species co-occur and interact with a wide array of other species during each life-history stage. Dominant mesopelagic species (Table 6) are not sampled by fisheries, and CalCOFI provides the only synoptic sampling of their populations. Our interpretation of the conclusions of Peterman et al. (1987) emphasizes predation during the late larval and prerecruit stages as a major determinant of recruitment. This occurs widely in the complex species assemblages sampled by CalCOFI surveys, and its relation to recruitment may be revealed by our correlation analyses in progress.

CONCLUSIONS

The early decades of biological oceanography in CalCOFI were marked by the identification of the oceanic regions and currents that impinged on the California coastal area. Johnson and Brinton (1965) used physical oceanography and analysis of planktonic species to describe the primary boundaries. The time series of the major epipelagic fish species—sardine and anchovy—by Murphy (1966) and Soutar and Isaacs (1974) have drawn attention to two scales of change: one at the scale of 3–5 years and another that acts over periods of 3–6 decades. Recent analyses of species assemblages (Moser et al. 1987) will offer time series comparisons for additional species at the decadal scale when the analyses under way are complete. In summary:

1. Spectral analysis of the fish-scale record indicates long-lasting population trends in sardine and anchovy and does not suggest equilibrium phenomena as population controls; the period of change is of the order of a half-century for several pelagic species.
2. The reproductive parameters of the northern anchovy show variations that are much less than the variations in specific recruitment rate.
3. Scale-deposition indices at two sites separated by 1000 km show little agreement, suggesting that the critical spatial scale of the events leading to species biomass changes is less than 1000 km.
4. Species biomass interactions among the major fish populations are weak at both scale-deposition sites.
5. Analysis of fish species assemblages suggests that predation by major mesopelagic species of the California Current region could affect survival rates of ontogenetic stages of epipelagic populations (e.g., sardine and anchovy) and thus influence recruitment variations.

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Over a dozen species of euphausiids from various parts of the world are known to appear in similar aggregations at the sea surface during the day (Komaki, 1967; Mauchline, 1980), but the frequency of swarming varies from species to species. *Euphausia superba* of the Antarctic may swarm at the surface during the day throughout most of its life cycle (Marr, 1962) and is the best studied euphausiid; other species, such as *T. spinifera,* appear to swarm only seasonally or intermittently (Mauchline, 1980). The mechanism that brings about the formation of these swarms is not clear and may differ according to species. Theories proposed to account for daytime surface swarming of various euphausiid species generally fall into the following categories: (1) the animals actively congregate at the surface for some biological purpose—to feed (Paulsen, 1909; Brown et al., 1979), reproduce (Ponomareva, 1966; Mauchline, 1980; Nicol, 1984a; Endo, 1984; Endo et al., 1985) or escape predators (Komaki, 1967); (2) they are passively transported to the surface by water currents or turbulence (Aitken, 1960; Forsyth and Jones, 1966; Brown et al., 1979; Terazaki, 1980); or (3) a breakdown of an environmental barrier, such as the thermocline, enables them to expand their vertical distribution to the surface (Komaki, 1967; Endo, 1984). These theories have proven difficult to substantiate since many aspects of the swarming phenomenon are not open to experimental investigation. Also, existing published accounts lack direct hydrographic evidence and comparative information on the vertical distribution of various components of the population before, during and after swarm activity.

It is not known which of the above factors are implicated in *T. spinifera* swarming activity, but the dominance of spent females in swarms that washed ashore in southern California (Boden et al., 1955) and Oregon (Pearcy and Hosie, 1985) suggests that swarming may be related to reproduction. In the more northern part of its range in subarctic waters, this species is reported to have a 2-year life cycle, reaching sexual maturity in its second year, with a one-time breeding season (Nemoto, 1957). Males must transfer a pair of spherical spermatophore packets to females for fertilization to take place, and in members of this genus, females shed their fertilized eggs freely in the water (Boden et al., 1955). The length of time between spermatophore transfer and release of eggs is not known.

The goal of the present study was to identify factors associated with swarming of *T. spinifera* off central California. We made observations of swarms and associated biological activity in a swarm area, collected oceanographic information, and examined samples from individual swarm patches and plankton collections obtained before, during and after swarm activity. In this paper, we describe our results and discuss the possible adaptive significance of swarming in this species.

MATERIALS AND METHODS

Swarms were observed and sampled between 1300 and 1530 h on 31 May 1985 in the Gulf of the Farallones (37°48.3′N, 122°56.3′W). Individual patches were sampled using a hand-held dip net (mouth area = 0.1 m^2, mesh width = 1.0 mm). Each sample came from a discrete patch, the size of which was estimated visually. These samples were then preserved in 10% neutralized formalin and seawater. Water temperature profiles were obtained with an expendable bathythermograph (XBT).

We were able to obtain depth-stratified plankton samples in the swarm area before, during, and after surface swarm activity. This was possible because the swarms occurred in the same area (within 1.5 km) in which we had been monitoring *T. spinifera* springtime relative abundance since 1983. A set of horizontal tows of 15-min duration was made at the swarm site 12 h prior to and 12 and 24 h after swarm activity was observed. Each set consisted of tows made at 55, 37, and 18 m over bottom depths of 68–70 m. During the day of swarm activity, one tow at 55 m was completed while dipnet samples were being collected from surface waters. These collections were made with an opening-closing Tucker net (described by Hopkins et al., 1973) with an effective mouth opening of 1 m^2 and a mesh size of 0.335 mm. The net was towed at 1.3 m sec^{-1}. Controlled test runs using a digital flowmeter in the mouth of the net indicated this procedure strained roughly 74 m^3 of water per minute, assuming

Table 1. Sex ratios, χ-square values, and significance levels of *Thysanoessa spinifera* swarm patch samples collected by dip net from the sea surface

Patch sample number	Patch area (m²)	N	% Females	χ^2	P
1	1.0	239	0.30	38.56	<0.01
2	1.5	136	0.31	19.12	<0.01
3	4.0	147	0.12	85.34	<0.01
4	1.5	133	0.38	6.76	<0.01
5	2.0	167	0.50	0.00	N.S.
6	3.0	154	0.65	13.16	<0.01
7	2.0	179	0.55	1.82	N.S.
8	5.0	116	0.76	30.02	<0.01
9	1.0	33	0.64	1.94	N.S.

the absence of net clogging. Organism counts were standardized for 1,000 m³ of water strained by the net.

Swarm samples containing 200 euphausiids or less were examined in their entirety; larger samples were divided with a Folsom plankton splitter. Total length was measured to the nearest millimeter from the tip of the rostrum to the tip of the telson. Body length, from the base of the eye to the junction of abdomen and telson, was also measured to allow comparison with other data. These lengths were highly correlated ($r^2 = 0.957$, $P < 0.0001$). A least-squares fit of 1,304 comparisons gave the equation

$$Y = 0.742X + 0.26$$

where Y = body length and X = total length. An analysis of variance showed that variation due to regression is significant, and therefore the true slope differs from zero ($F = 29{,}051$; df = 1,1302; $P < 0.001$). Females were classified as (1) with spermatophores attached, with ripe or ripening eggs (0.2–0.4 mm in diameter); (2) without spermatophores, with ripe or ripening eggs; (3) without spermatophores, with early developing eggs (<0.2 mm); and (4) with spermatophores attached, but with no eggs discernible in the thoracic cavity (spent). Females with spermatophores attached to the thelycum will be termed "fertilized," even though actual fertilization of eggs may not take place at the time of spermatophore transfer. Males were classified as (1) with ripe spermatophores protruding or internal; and (2) without ripe spermatophores. All specimens were grossly examined for the presence of parasites. In addition, the ventral food basket between the thoracic appendages of each specimen was examined, and contents of food boluses were identified to the lowest possible taxonomical level.

RESULTS

Nine patches, 1–5 m² in size (Table 1), each approximately 137 m apart, were sampled over an area of about 1 km². The aggregations occurred from the surface to a maximum depth of about 37 m in 71 m of water, based on echosounder readings (Fig. 1A).

Weather and sea conditions at the swarm site were seasonally mild: wind speed = 8 knots, wind direction = 270°, sea state = 2 on Beaufort scale, swell height = 1 m, swell direction = 255° mag., cloud cover = 2 (⅛ sky covered). During the cruise period (30 May–5 June), oceanographic conditions were characterized as transitional, marked by persistent south winds, relaxation of upwelling, and warming and stratification of upper surface layers.[1] Coastal Upwelling Index values (Bakun, 1975) for the central California coast were well below average for the last week in May, indicating an absence of strong upwelling during and preceding swarm activity.[2]

Observations of swimming behavior and patch shape were made while the ship

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[1] K. Briggs. University of Santa Cruz, Santa Cruz, CA 95064, pers. commun. June 1985.

[2] Andrew Bakun, Pacific Fisheries Environmental Group, National Marine Fisheries Service, NOAA, Monterey, CA 93942. Unpubl. data.

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DAYTIME SURFACE SWARMS OF *THYSANOESSA SPINIFERA* (EUPHAUSIACEA) IN THE GULF OF THE FARALLONES, CALIFORNIA

Susan E. Smith and Peter B. Adams

ABSTRACT

Daytime surface swarms of the euphausiid *Thysanoessa spinifera* were observed and sampled in spring 1985 in the Gulf of the Farallones off San Francisco, California. Samples were dipnetted at the surface from nine discrete swarm patches; and depth-stratified plankton tows were made before, during, and after swarm activity. Analyses of sex and maturity stage of surface patch samples showed that 94% of all euphausiids were in breeding condition. Sex ratios differed significantly in six of the nine patches, with males dominating four and females dominating two patches. This sexual segregation is thought to be related to differences in size between sexually mature males and females. Biological and oceanographic observations at the swarm site, and examinations of food baskets of swarm individuals, gave little indication that the animals were passively transported to the surface, or that they were there to feed or avoid predators. *T. spinifera* eggs and Stage 1 nauplii were numerous in plankton collections taken the night following, and day after surface swarming was observed. It is concluded that swarming in this species is related to reproduction. Its adaptive value in regard to different breeding-related activities is still unclear, but probably involves a combination of factors that relate to the timing of sexual maturation, egg release, and larval dispersal in the changeable upwelling environment off central California.

The neritic euphausiid *Thysanoessa spinifera* aggregates in conspicuous daytime swarms at the ocean surface along the California coast during spring and summer. Little is known about these surface swarms or what triggers their formation, probably because of the unpredictable nature of their onset and duration. The behavior occurs during daylight when most vertically migrating euphausiids, including *T. spinifera* (Alton and Blackburn, 1972), are usually found at greater depths.

In general, upwelling centers have been associated with highest densities of *T. spinifera* (Brinton, 1962); and in the Gulf of the Farallones, daytime swarms occur sporadically from about April to July, when upwelling events are the most frequent and intense along the central California coast (Bakun, 1975). During this time, northwest winds intensify, triggering the offshore transport of warm surface waters, which are then replaced by cool, nutrient-rich water from the depths (Bolin and Abbot, 1962). Periodically during the upwelling season, northwesterly winds slacken, the process temporarily subsides, and surface temperatures may rise due to solar radiation or intrusion of warmer offshore water (Bolin and Abbot, 1962; Hatfield, 1983).

When the rust-colored patches appear, many of the commercial sport fishing boats, guided by flocks of feeding seabirds, seek them out in search of salmon, which we have found to feed heavily on euphausiids at this time of year. Although this daytime swarming is often highly visible and appears to be a relatively common event off central California, very little information is available on swarm population structure. The only published reports consist of brief accounts of swarms that washed ashore at La Jolla, California (Boden et al., 1955), and Bandon, Oregon (Pearcy and Hosie, 1985), which were composed entirely of spent females, and those observed in Monterey Bay by Barham (1956) for which sex and maturity composition are not known.

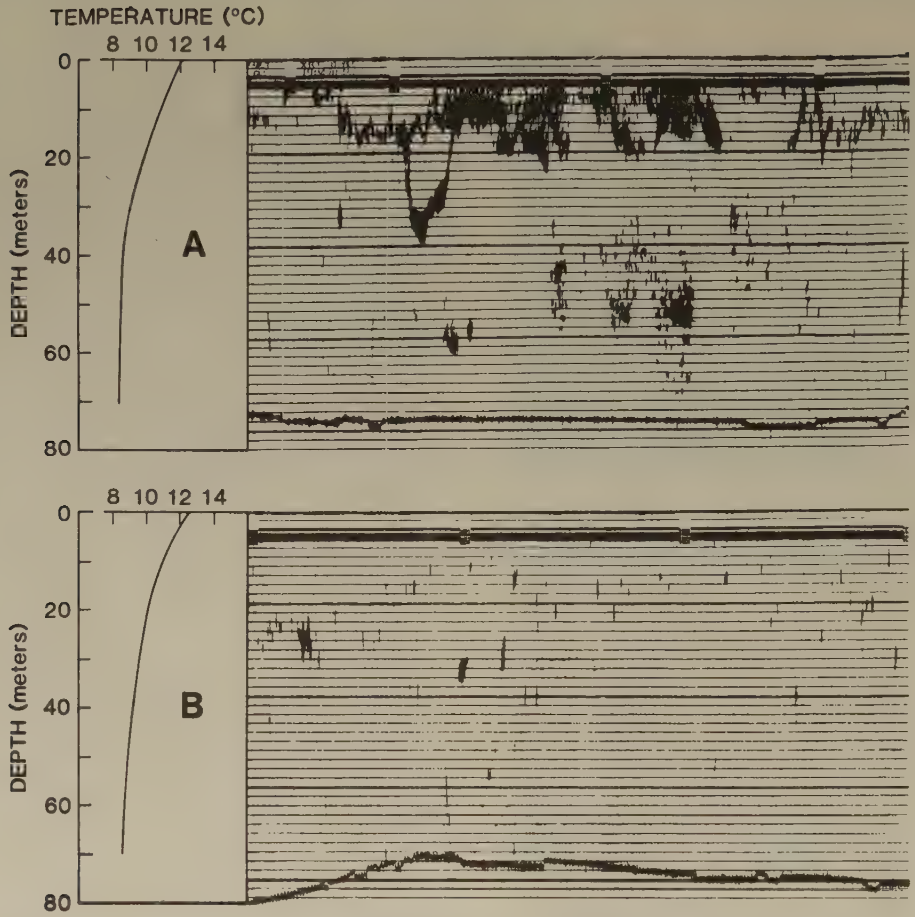

Figure 1A. Echogram (38 kHz) and XBT temperature profile obtained at the surface swarm site on the day of swarm observations, 31 May 1985; Figure 1B. Echogram and XBT temperature profile obtained at the surface swarm site the night following swarm activity, 1 June 1985.

drifted into the swarming area and during sampling. Some of the patches were roughly circular and contained tightly spaced individuals without parallel orientation. Others were ribbonlike streams of individuals, which swam parallel to each other at an estimated 0.3 m sec^{-1}. The animals often sounded rapidly as a group when disturbed, and some individuals even vaulted from the water in an effort to escape the dip net or the samplers' boat. Isolated individuals were also observed swimming at the surface outside the dense patches.

Although feeding activity of fishes has been associated with surface swarming of *T. spinifera* in Monterey Bay (Harvey[3]) and in the Gulf of the Farallones (by the salmon sportfishing fleet[4]), we saw no evidence of this at the swarm site. The

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[3] Harvey, J. T. Daytime surface swarming of euphausiids in Monterey Bay, California. Unpubl. manuscr., Hatfield Marine Science Center, Oregon State University, Newport, OR 97365.

[4] Roger Thomas, Captain *Salty Lady*, Harbor Drive, Sausalito, CA 94965, pers. commun. May 1985.

Table 2. Estimated number per 1,000 m³ (N) and percent sample volume (%) of *T. spinifera* eggs, nauplii, and adults taken in plankton tows at the swarm site before, during, and after swarm activity

Tow depth (m)	Tow duration (min)	Eggs		Nauplii		Adults			Total sample volume (ml)
		N	%	N	%	Ripe ♂	Fert. ♀	%	
Night before swarm activity (0150–1340 hr)									
18	15	19,533	0.01	—	—	91	40	0.12	183
37	16	744	<0.01	—	—	18	10	0.05	94
55	15	689	<0.01	—	—	15	1	0.05	56
Day of swarm activity (1400 hr)									
55	15	3,217	<0.01	64	<0.01	—	*	—	109
Night following swarm activity (0200–0350 hr)									
18	15	17,235	0.05	—	—	3	3	0.01	63
37	15	28,151	0.20	—	—	—	2	0.01	43
55	15	18,269	0.13	—	—	1	1	0.01	31
Day after swarm activity (1240–1400 hr)									
18	15	4,600	0.01	1,181	<0.01	—	—	—	47
37	15	24,129	0.30	—	—	—	—	—	23
55	15	9,566	0.07	—	—	—	—	—	46

* A single, unfertilized female with early stage eggs was taken in this collection.

only predators evident in the area were western gulls (*Larus occidentalis*) which were observed on the water singly or in pairs, feeding on individual patches.

There was no evidence, either in our plankton collections (Table 2) or in echosounder tracings (Fig. 1B), that the surface swarming persisted after nightfall. Euphausiid eggs, however, were numerous in plankton collections taken that night and the next day (Table 2). Although positive identification could not be made of the eggs or of the Stage 1 nauplii found in near-surface samples the following day, the size of the egg embryos and the shape of the nauplii differed from those of *Euphausia pacifica*, the only other abundant euphausiid in the area.[5] We therefore assume that the eggs and nauplii were those of *T. spinifera*. Egg numbers may have been underestimated because of possible extrusion through the net meshes (mean egg diameter = 0.41 mm; mesh width = 0.335 mm; mean diagonal mesh width = 0.42 mm).

Analyses of sex and maturity stage of the dipnetted samples from surface patches showed that 94% of all euphausiids were either males with fully developed spermatophores or fertilized females with ripe or ripening eggs. The sex ratio, however, differed from patch to patch. Six of the nine collections differed significantly from the expected 1:1 male : female ratio, with males dominating in four collections and females dominating in two collections (Table 1). Analyses of length frequencies by maturity stage helped to distinguish major components of the swarms (Fig. 2). Overall, sexually mature males (TL mean = 20.7 mm) and large fertilized females with eggs (TL mean = 25.4 mm) comprised 55.7% and 38.0%, respectively, of the sampled population. A third, lesser group (4.8% of individuals), which occurred strongly only in patch sample 2, was composed of smaller developing females (TL mean = 19.9 mm). The remainder (1.5%) consisted of unfertilized ripe females (8 individuals), spent females (6), and males without spermatophores (5).

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[5] Margaret Knight, Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun. March 1986.

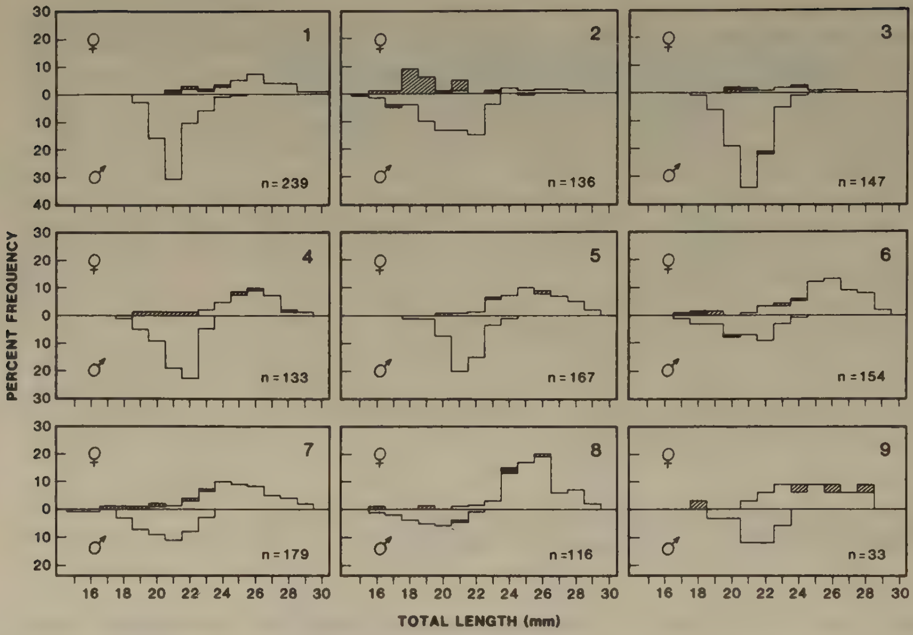

Figure 2. Length frequency histograms of the nine sampled swarm patches of *Thysanoessa spinifera*. Crosshatching = unfertilized developing females; open = fertilized females with ripe or ripening eggs and males with spermatophores; solid = other (males without spermatophores, fertilized females without eggs, and ripe, unfertilized females).

Examination of food baskets of swarm individuals indicated little feeding activity, but some cannibalism was evident. The only recognizable items were euphausiid ommatidia and other optic material. Of the 1,304 specimens examined, 81.1% had empty food baskets, 17.6% contained euphausiid ommatidia, and the remainder contained unrecognizable material.

Suctorian protozoans infested the exoskeletons of 75.2% of the euphausiids examined.[6] The thoracic cavity of three female individuals each contained a single larval nematode, identified as *Anisakis* sp.[7]

DISCUSSION

The results provide evidence of sexual segregation in *T. spinifera* and strongly indicate that swarming is related to reproduction. It is unlikely that the euphausiids were transported to the surface by some physical force, judging from the stratified temperature profiles and mild oceanographic conditions, and we found no evidence that they were there to feed or avoid predators.

Some of these findings are very similar to those of others who have recently studied daytime swarming of temperate water euphausiids on other coasts. Nicol (1984a) found that reproductive adults dominated swarms of *Meganyctiphanes norvegica* in the Bay of Fundy, and that sex ratios from patch to patch were highly skewed. He also found a high degree of suctorian infestation in swarm samples compared to those taken at depth offshore (Nicol, 1984b). Endo (1984) and Endo et al. (1985) concluded that swarming of *Euphausia pacifica* in Sendai Bay, Japan, was related to reproduction, although the majority of ripening females they sampled were as yet unfertilized. They also found a predominance of euphausiid spines and eye parts in guts of swarm individuals and a similar infestation of suctorian epibionts.

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[6] Identified by S. K. Johnson, Texas A&M University, 111 Nagle Hall, College Station, Texas 77843, pers. commun. May 1986.

[7] Identified by Mike Moser, University of California, Santa Cruz, CA 95064, pers. commun. April 1986.

Adult male euphausiids and the larger adult females may segregate by sex to facilitate schooling (Nicol, 1984a). Those patches in which the sexual segregation was not pronounced may represent the convergence of male and female aggregations and, indeed, swarm patches have been seen to merge and separate.[8] The fertilized mature females and sexually mature males are assumed to represent the 1983 year class because they correspond to individuals classified as Age 2 by Nemoto (1957). If so, the smaller developing females are likely sexually precocious individuals of the 1984 year class. Their association with the more sexually advanced males may be based on corresponding size and therefore swimming efficiency, rather than corresponding reproductive stage.

Surface swarming may relate to reproduction in one or more of the following ways: (1) for more effectual transfer of spermatophores from males to females, (2) for release of eggs at the surface, or (3) for maturation of sexual products in adults and/or incubation of eggs in warm surface layers. There are arguments for and against all of these possibilities.

Swarming for the purpose of spermatophore transfer seems likely, considering the range of sex ratios in individual patches and observations of swarms merging. But the virtual absence in our samples of mature but as yet unfertilized females suggests otherwise. We have also found a similar absence of unfertilized females in plankton samples and chinook salmon (*Oncorhynchus tshawytscha*) gut contents collected throughout the swarm season. This suggests that the bulk of spermatophore transfer takes place prior to the surface swarming season, and that refertilization of molted females, if it does occur, takes place in areas less accessible to our collecting gear and to salmon predation. Nicol (1984a) also found very few unfertilized mature females in swarming *Meganyctiphanes norvegica* in the Bay of Fundy.

Although the intermolt period for nonreproductive *T. spinifera* has been estimated at 5 to 6 days (Jerde and Lasker, 1966), molting may be delayed or suspended during the reproductive period or upon reaching sexual maturity (Dexter, 1977; Nicol, 1984b). This would further explain why an overwhelming majority of females carry intact spermatophores throughout the breeding season, and may account for the high incidence of exoskeleton infestation by suctorians. Suspension of ecdysis would seem an adaptive means to alleviate the need for segregated males to relocate and refertilize females with each molt.

The presence of eggs in the swarm area suggests that egg release may be an important function of swarming. This hypothesis is supported by the reports of swarms composed entirely of spent female *T. spinifera* (Boden et al., 1955; Pearcy and Hosie, 1985). Egg incubation, however, is probably not a factor, since euphausiid eggs, being denser than seawater, tend to sink when broadcast freely in the sea (Mauchline and Fisher, 1969). Even so, neritic species such as *T. spinifera* would benefit from releasing eggs high in the water column, thus providing more time for eggs to develop and hatch before reaching the sea floor. After hatching, the larvae are thought to ascend to surface waters where food supplies are abundant

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[8] Peggy Gamin, vessel *Salty Lady*, Harbor Drive, Sausalito, CA 94965, pers. commun. May 1985.

(Mauchline and Fisher, 1969) and the greater average velocity of surface currents can disperse them away from the area and potential cannibalism by adults. But the advantage gained by suspending or reversing normal diel migratory behavior by aggregating at the surface during daylight hours is still not clear. As with other breeding-related activity, egg release could occur during crepuscular or nocturnal periods, presumably with the same benefits mentioned above with the added protection from diurnal predators that darkness would provide. In addition, less than 1% of females in our swarm samples were spent, which indicates that egg release may not be the primary swarm activity during the day, or at least during the afternoon period that we sampled.

Perhaps one of the functions of daytime surface swarming is to prolong exposure of reproductive individuals to the warmer surface layers, where maturation of sexual products would be accelerated. Lindley (1978), working with *Thysanoessa longicaudata,* found that timing of reproduction in spring was correlated with sea surface temperature, and concluded that the rate of sexual maturation is controlled mainly by temperature. The animals may take advantage of interim warming periods between upwelling events to accelerate gonadal development in the warm surface layers. But again, the advantage gained by this strategy would have to outweigh the disadvantage of being highly vulnerable to predation at the sea surface during the day.

Most likely, the adaptive significance of *Thysanoessa spinifera* surface swarming encompasses more than just one factor, since the selective forces acting upon breeding adults would differ from those acting upon eggs and larvae (Dingle, 1980). Both the timing of sexual maturation and the timing of egg release and subsequent larval dispersal would seem crucial, since these events occur during the upwelling season when water temperature and sea surface current velocity and direction can change over a short period of time. Success, however, would seem to depend largely on the rapid behavioral responses of breeding adults. Swarming may be such a response. Although the cost of being at the surface in daylight would seem high for adults because of their greater visibility, the intermittent formation of dense schools, and the rapid response to stimuli that schooling facilitates, may offer the needed edge over predators to ensure that sufficient numbers of adults survive to breed and release their eggs under favorable environmental conditions. The small-scale patchiness revealed by this study re-emphasizes the importance of direct sampling of these reproductive swarms, the dynamics of which may be masked by more conventional sampling with towed plankton nets.

ACKNOWLEDGMENTS

We are grateful to D. Ainley and R. Ferris of the Point Reyes Bird Observatory for their help in obtaining surface swarm samples, and to D. Ainley, E. Brinton, J. Chess, Y. Endo, J. Harvey, E. Hobson, M. Knight, and S. Nicol for their constructive comments on earlier drafts of the manuscript.

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Hook Timers to Measure the Capture Time of Individual Fish

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ABSTRACT—*To measure capture time of individual fish on a longline, two types of hook timers installed in the leaders and activated by a striking fish were designed and tested: 1) A corrosion timer that measures time indirectly from the mass loss of the anode in a galvanic corrosional reaction and 2) a digital timer that measures time directly by a digital watch module. The digital timer proved to be superior because it is reusable, quicker to deploy and retrieve, and measures time directly with little error.*

Introduction

Gear saturation and interspecific competition for hooks complicate the use of longlines for stock assessment. Gear saturation occurs when fish density is so high the proportion of unoccupied, baited hooks approaches zero before the longline is retrieved. If this occurs, catch is not a continuously increasing function of time, and catch per unit effort (CPUE) is not proportional to abundance (Ricker, 1975). Interspecific competition for hooks occurs when the CPUE of one species is reduced by the catch of other species on the same longline. Such an effect is especially pronounced when the gear approaches saturation (Rothschild, 1967).

These problems led us to search for other ways of using longlines to estimate relative abundance, and from a theoretical standpoint, the most promising alternative was a method based on the time required to hook each fish (Somerton[1]). The abundance estimates used by this method are unaffected by gear saturation because they are completely determined when the last fish is caught. The estimates are also unaffected by interspecific competition, as long as one species does not physically exclude another from taking the hook, because they are computed for all species jointly.

This method requires development of a small, inexpensive timing device that will activate when the hook is struck by a fish. We describe and test two different designs for such a device: A corrosion timer and a digital timer.

Methods

Corrosion Timer

The corrosion timer is based on the principle that, when two dissimilar metals are connected electrically and placed in seawater, a galvanic cell is created and one of the metals (anode) is ionized. The exposure time to seawater can be estimated from the anode mass loss, which depends on the electromotive potential of the two metals, the size and shape of the anode and cathode, and the salinity and temperature of the seawater (Loose, 1948). For our objectives, the corrosional reaction had to be consistent from one timer to the next and rapid enough so that mass loss in a 15-minute period is sufficient to be easily detectable but not so rapid that the anode corrodes completely in <4-6 hours.

The anode was a 38 mm long × 3.9 mm diameter magnesium welding rod (93.3 percent Mg, 5.5 percent Al, 1.0 percent Zn, 0.2 percent Mn); the cathode was two 25 mm stainless steel (304 grade) fender washers secured by stainless steel nuts to the threaded ends of the welding rod (Fig. 1). To isolate the timers from seawater until the hooks were struck by fish, they were placed in watertight containers (35 mm film cannisters) attached to the leaders (Fig. 2). The rims of the cannister openings were sanded until the caps released with 1 kg of pull, a tension weak enough for the cannisters to be opened by all target species yet strong enough that few opened accidentally as the longlines were set. In addition, the cannisters were filled with a 1:1 mixture of distilled water and isopropyl alcohol to prevent them from collapsing under hydrostatic pressure and thereby changing the activation tension.

Anode mass loss as a function of exposure time was initially estimated in the laboratory. Twenty-four timers were placed simultaneously in seawater (salinity, 34.7‰; temperature, 23.5°C) in a 4,000-liter tank and removed, three at a time, at 15-minute intervals for up to 2 hours. The resulting mass loss was linear with time, and variability among replicates was so low that there was no overlap in mass loss between adjacent 15-minute intervals (Fig. 3). Although additional laboratory calibration experiments were run at approximate in situ temperatures and salinities, we suspected that pressure (the timers were intended to be used at <1,000 m depths),

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[1] Somerton, D. A. A method of stock assessment using the time-to-capture of individual fish on a longline and its application to pelagic armorhead, *Pseudopentaceros wheeleri*, on the Hancock seamount. Manuscr. in prep. Honolulu Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 95822-2396.

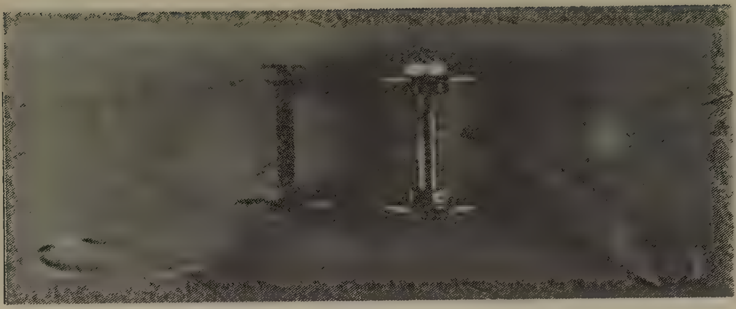

Figure 1.—Corrosion timers before (right) and after (left) exposure to seawater for 2 hours. Note the loss of material from the anode (central rod) and the deposition of material on the cathode (end pieces).

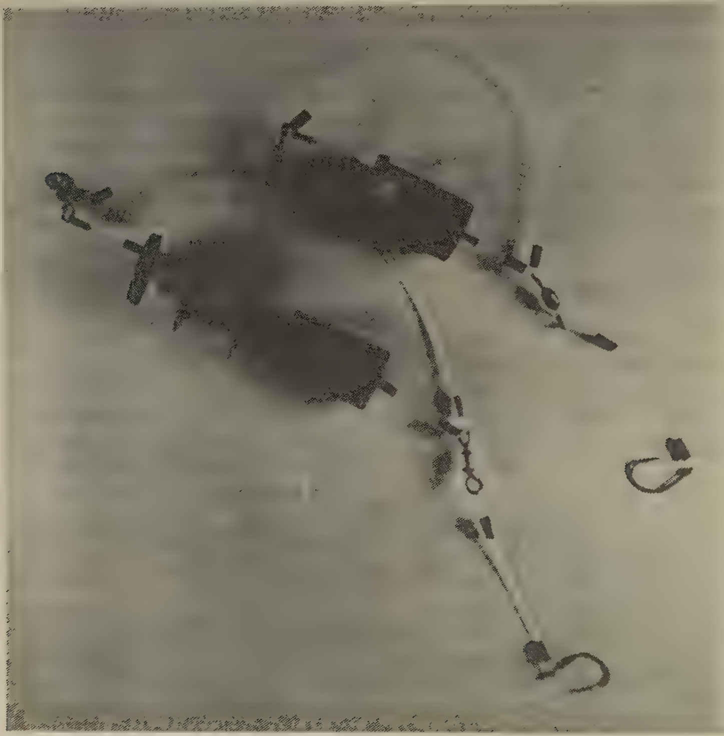

Figure 2.—Corrosion timer cannisters as they would appear when the longline is set (upper) and after a fish has struck the hook (lower).

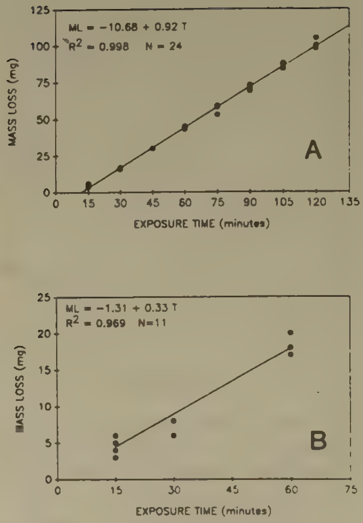

Figure 3.—Anode mass loss of corrosion timers and exposure time to seawater: A) in a laboratory experiment (salinity, 34.7‰; temperature, 23.5°C) and B) at the Hancock Seamount (salinity, 35.0‰; temperature, 15.5°C).

dissolved oxygen concentration, and water movement would likely affect the corrosion rate.

We therefore attempted an in situ calibration by exposing the timers to seawater (salinity, 35.0‰; temperature, 15.5°C) at depth by using a shipboard water sampling rosette. The one successful in situ calibration showed greater variability in mass loss than did the laboratory calibrations, and perhaps some nonlinearity with time (Fig. 3); however, the linear fit of the data was sufficiently good that the in situ calibration rather than the laboratory calibrations was used in the field tests.

Digital Timer

The digital timer (65 mm long × 29 mm diameter) consisted of a digital clock module with a liquid crystal display (Sterling Electronics, Taipei, Taiwan[2]), an alkaline disc battery, and a magnetic reed switch (single pole double throw; Hermetic Switch, Inc., Chickashs, OK 73018), which were enclosed in metal hardware cloth and embedded in a cylinder of polyester casting resin (Fig. 4). A hole at one end of the cylinder contained a ceramic magnet used to activate the reed switch (Fig. 4). When the magnet was pulled out of the hole, the reed switch closed and the digital clock started from its reset value of 1:00; when the magnet was reinserted, the clock was reset. The pull required to activate the digital timers was standardized to 1 kg by an adjustable, spring-loaded pin assembly that rested against the magnet (Fig. 4). The rigidity of the timer was sufficient to withstand short-term (about 5-minutes) exposure to chamber pressures equivalent to 1,000 m in depth. The reed switch was partially shielded from external magnetic fields with metal hardware cloth to minimize the chance of the timers being accidentally reset by a struggling fish. Ceramic magnets and stainless steel springs and pins were used to prevent corrosion of either the magnet or the spring-loaded pin assembly that could potentially alter the activation tension of the timer.

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[2] Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

Field Trials

All field trials were conducted on the Southeast Hancock Seamount (lat. 29°48′N, long. 179°E) at depths of 250-800 m. The primary fish species encountered here is pelagic armorhead, *Pseudopentaceros wheeleri*, a small (≈1 kg), sluggish species often forming dense aggregations near the summit.

The timers were tested, based on handling time and failure rates, with Kali longlines, a fishing gear used repeatedly for stock assessment of pelagic armorhead (Shiota[3]). This gear consisted of rigid poles (droppers) snapped on a groundline at 20 m intervals. Each dropper (3.2 m long) had five hooks on short, equally spaced leaders and was weighted so that it was positioned vertically while fishing. The only modification to this gear was the replacement of the normal leaders with leaders having timers spliced in (Fig. 5).

Corrosion timers were field tested once in July (N = 3,264) and once in October 1986 (N = 1,332). Droppers with and without timers were alternated on the groundline to assess the influence

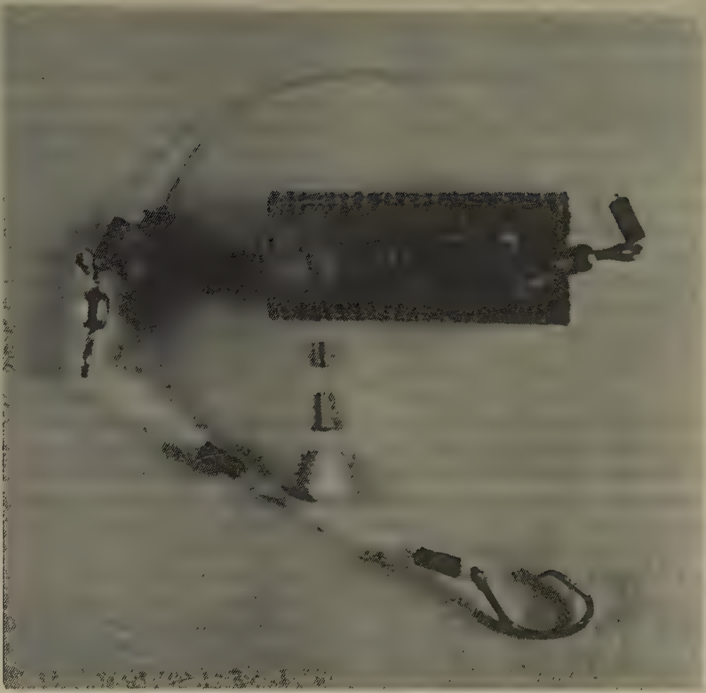

Figure 4.—Digital timer as it would appear 9 minutes after being struck by a fish.

Figure 5.—Corrosion timers in use. Note that the hook leaders are attached to a rigid pole rather than directly to a groundline.

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[3] Shiota, P. M. 1987. A comparison of bottom longline and deep-sea handline for sampling bottom fishes in the Hawaiian Archipelago. Honolulu Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 95822-2396. Southwest Fish. Cent. Admin. Rep. H-87-5, 18 p.

of timers on fishing characteristics of the gear. In the first field test, the corrosion timers sustained accidental damage severe enough to invalidate the mass loss weights; therefore, statistical tests involving time information omit the first trial. Digital timers were field tested in August 1987 (N = 3,840); no side-by-side comparisons were made.

The general times and procedures for using the longline gear were as follows: 1) Baiting hooks (20 minutes), 2) setting (10 minutes), 3) soak time (60 minutes), and 4) retrieval and recording the catch data (30 minutes). The use of hook timers required additional procedures. Corrosion timers were attached to cannisters with monofilament leashes (Fig. 2); cannisters were closed while immersed in an alcohol and water mixture. Upon retrieval, individual corrosion timers were removed and placed into a bucket of alcohol to slow corrosion and, after complete recovery of the longline, were air dried and separated from the cathodes to stop corrosion. In the laboratory, corroded anodes were washed, dried, and weighed to the nearest milligram, and the exposure times were estimated by using a previously determined time and mass loss function. For digital timers, the display was read immediately when the gear was brought aboard the vessel, and the timer was reset later by reinserting the magnet into its retaining hole.

Results

Hook timers tended to affect preparation and processing times more than setting and retrieval times. For corrosion timers, attaching new timers increased gear preparation time by about 100 percent, and depending on the size of the catch, deactivating the timers increased processing time by up to about 50 percent. For digital timers, the resetting process increased gear preparation time by about 15 percent, but all other times were unaffected.

Longlines with timers were subject to a variety of failures in addition to the usual modes of failure of the unmodified longlines (e.g., hook loss, bait loss), resulting in losses of time data and sometimes species identity. Two types of failure were premature activation and nonactivation of timers. Premature activation occurred when the timers were prepared improperly (e.g., cannisters not closed completely, magnets not inserted sufficiently to deactivate the reed switch) or were activated accidentally prior to setting. Nonactivation occurred when a fish was too small or too sluggish to activate a timer.

Our experience with both of these failures was as follows: For corrosion timers, 5 percent of 547 activated timers (October 1986 data only) were premature and 16 percent of 1,260 captured fish failed to activate the timers; for digital timers, 6 percent of 2,185 activated timers were premature and 7 percent of 700 captured fish failed to activate the timers. These modes of failure are influenced by the tension required to activate the timers: Increasing tension decreases premature activation but increases nonactivation. The appropriate tension, one balancing these two modes of failure, is a function of the size and activity of the target species and may only be an important consideration for such species as armorhead that are relatively small and sluggish.

Another type of failure was simple mechanical failure or breakage. Corrosion timers rarely failed in this manner, but leashes (Fig. 2) broken when the timer was snagged during recovery resulted in the loss of 13 percent of 1,281 activated timers. We believe this failure rate can be reduced by increasing the strength of the leashes. Digital timers were subject to several types of mechanical failure. Some liquid crystal displays became totally or partially blackened and unreadable after prolonged exposure to direct sunlight and high deck temperatures. Repeated use of timers at ≥500 m depths sometimes resulted in a total loss of power to the display or a malfunction of one or more digits on the display. The ceramic magnet sometimes fractured when struck on the deck. Although these failures, taken together, resulted in a loss of 50 percent of the 300 digital timers used in the field trials, each timer was used an average of 19 times before failure occurred, and such failures resulted in a loss of only 7 percent of the 2,185 times obtained. We believe the failure rate of digital timers can be reduced by shielding them from direct exposure to sunlight and casting the electronic components in either a harder or larger cylinder of resin.

In addition to data losses attributable to timer failures, we probably also lost data on species identity if timers were activated by fish not subsequently caught. The frequency of activated timers without fish was quite high: 42 percent of 1,831 activated corrosion timers and 70 percent of 2,185 activated digital timers. Although data are not sufficient to determine whether these hooks were actually struck by fish or were snagged on an object, we speculate that the momentary drop in tension that occurs when a timer is activated may decrease the likelihood of catching a fish.

We examined this possibility by comparing the proportion of hooks recovered with fish for the gear with and without corrosion timers. Thirty-eight percent of 3,337 hooks with timers caught fish, whereas 46 percent of 3,347 hooks without timers caught fish. Although hooks without timers caught significantly more fish ($\chi^2 = 46.1$, $P < 0.01$), it is not clear whether this gear was more attractive and had a higher rate of strikes than timer gear or had a higher retention rate when struck. If all hooks without bait presumably were struck, then 49 percent of 2,519 strikes on hooks with timers retained fish compared with 58 percent of 2,674 strikes on hooks without timers. Thus, the retention rate is significantly lower for hooks with timers ($\chi^2 = 34.0$, $P < 0.01$) and is likely responsible for the relatively low occupancy rate of activated timers. We believe the failure of timer gear to hook fish is, like timers prematurely activated, potentially preventable by increasing the activation tension.

Discussion

Although the abundance estimates we use for stock assessment require time-to-capture data (Somerton[1]), both timers are activated when fish strike and, therefore, measure time-since-capture data. For work in shallow water, time to capture can be calculated by subtracting time since capture from total elapsed time (surface to surface). For armorhead, however, fishing is conducted at depths of 250-900 m, so time to capture must be corrected for sinking time of gear. Currently, we estimate sinking time with time and depth recorders (Wildlife Computers, Woodenville, WA 98072) attached to the longline, but are considering a modified digital timer, attached to the base of a dropper, that will be activated when the gear hits the bottom.

We now use digital timers exclusively in our armorhead stock assessment because they are preferable to corrosion timers in three respects. First, digital timers are reusable and, if gear loss is low and reuse is high, are cheaper than corrosion timers to collect equal sample sizes. Second, digital timers require less time to set and retrieve than corrosion timers and require no additional processing time. Third, digital timers are more precise because time is measured directly rather than estimated from mass loss. Digital timers, however, are made from parts that may be difficult to obtain and that require skill and specialized equipment to assemble, whereas corrosion timers are made from inexpensive, readily available materials and can be fabricated by inexperienced personnel.

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Molecular Characterization of a Cloned Dolphin Mitochondrial Genome

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Summary. DNA clones have been isolated that span the complete mitochondrial (mt) genome of the dolphin, *Cephalorhynchus commersonii.* Hybridization experiments with purified primate mtDNA probes have established that there is close resemblance in the general organization of the dolphin mt genome and the terrestrial mammalian mt genomes. Sequences covering 2381 bp of the dolphin mt genome from the major noncoding region, three tRNA genes, and parts of the genes encoding cytochrome b, NADH dehydrogenase subunit 3 (ND3), and 16S rRNA have been compared with corresponding regions from other mammalian genomes. There is a general tendency throughout the sequenced regions for greater similarity between dolphin and bovine mt genomes than between dolphin and rodent or human mt genomes.

Key words: D-loop sequence — Similarity blocks — Sequence evolution — Conservation of genome organization

Introduction

Valuable information about phylogeny and the speciation process in primates (Ferris et al. 1981; Brown et al. 1982), ungulates (Higuchi et al. 1984; Watanabe et al. 1986), rodents (Ferris et al. 1983; Lansman et al. 1983), birds (Shields and Wilson 1987), reptiles (Wright et al. 1983), and amphibians (Spolsky and Uzzell 1984) has been provided by analysis of sequence variability in the animal mitochondrial DNA (mtDNA). The complete nucleotide sequences of human, murine, and bovine mtDNAs have identified unique characteristics of mammalian mtDNA including compact and efficient gene arrangements, specific codon usage, and a high mutation rate (Brown et al. 1979; Anderson et al. 1981, 1982; Bibb et al. 1981). In addition to the structural genes, the animal mitochondrial (mt) genome contains a large noncoding region, including the displacement loop or D-loop, that comprises 5–7% (approximately 800–1200 bp) of the genome. Length variations in the D-loop region account for virtually all of the size differences between human, murine, and bovine mtDNAs. The noncoding region appears to encode regulatory functions for the expression of mt structural genes and replication of the heavy strand (Ojala et al. 1980; Olivo et al. 1983; Chang and Clayton 1984; Chomyn et al. 1985). However, at present, there is only limited information relating to the structural organization of putative regulatory signals within the D-loop region and the controlling mechanisms for mt replication and gene expression.

We have studied two dolphin species: *Cephalorhynchus commersonii* (Commerson's dolphin) and *Delphinus delphis* (common dolphin). The Commerson's dolphin is found exclusively in the southern coastal waters of Argentina and Chile and around the Falkland Islands in the Atlantic Ocean as well as the Kerguelen Islands in the Indian Ocean, whereas the common dolphin is found in temperate and tropical waters around the world. The *C. commersonii* mtDNA described here is representative of the mt genome of an individual animal living in a natural environment. The nucleotide and amino acid

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sequence comparisons with terrestrial mammalian mtDNAs have provided information about the conservation of regulatory signals and functional domains in proteins from a mammal adapted for life in a marine environment.

Materials and Methods

Preparation of mtDNA. Samples of *Delphinus delphis* liver were obtained from a dolphin that had been stranded on a California beach. The *Cephalorhynchus commersonii* liver sample was obtained through the Hubbs Marine Research Institute and Sea World in San Diego and came from the natural population of Commerson's dolphins living off Tierra del Fuego. The dolphin mtDNAs described here can therefore be regarded as representative of wild-type genomes.

Supercoiled mtDNA was prepared from frozen liver tissue of *Cephalorhynchus commersonii* and *Delphinus delphis.* The tissue was disrupted in a high-EDTA buffer (10 mM Tris-HCl, pH 7.3, 0.25 M sucrose, 75 mM EDTA) using an Omnimixer blender and a Dounce homogenizer, followed by removal of whole cells and nuclei by low-speed centrifugation. Mitochondria were pelleted by high-speed centrifugation, lysed with 2% SDS, and the supercoiled mtDNA was purified by propidium di-iodide–CsCl equilibrium density gradient ultracentrifugation. A typical yield was 5–10 μg of supercoiled mtDNA from 20 g of liver tissue.

Construction and Characterization of mt Clones. Preparations of purified supercoiled mtDNA were digested with *Eco*RI or *Bam*HI and ligated with predigested phage (Charon 28) and plasmid (pBR322, pRK404, and pACYC184) vectors. In each case, the vectors were treated with calf intestinal alkaline phosphatase to minimize the re-ligation of vector molecules without insert sequences. Standard transfection and transformation procedures were used to regenerate phage and bacterial stocks. Following antibiotic selection, clones were screened for the presence of mtDNA inserts by plaque and colony hybridization techniques using purified dolphin mtDNA as a probe. Some regions of the mt genome were not recovered when unfractionated restriction digests were ligated directly to the vectors. We therefore purified individual restriction fragments by preparative agarose gel electrophoresis and electro-elution prior to ligation with the stringent, low-copy number plasmids pRK404 and pACYC184. This approach allowed the cloning of restriction fragments covering the entire *C. commersonii* mt genome.

Hybrid plasmid DNAs were purified from bacterial cell cultures using techniques of Triton X-100/lysozyme lysis and equilibrium density gradient centrifugation with CsCl and ethidium bromide. Detailed restriction maps of the mt sequences were derived, and this information was used in the design of nucleotide sequencing experiments. We used the chemical sequencing technique of Maxam and Gilbert (1980) in conjunction with 5′ and 3′ end-labeled restriction fragments. All sequences were derived independently from both DNA strands.

Hybridization Reactions with Primate mt Probes. Purified restriction fragments of primate mtDNAs were labeled by nick translation in the presence of α^{32}P-dATP and α^{32}P-dCTP to obtain specific activities of $3–5 \times 10^8$ cpm/μg. The probes were cloned fragments of mtDNA from gorilla and pygmy chimpanzee (gift from Dr. W.M. Brown, Laboratory of Molecular Systematics, University of Michigan, Ann Arbor, Michigan 48109, USA). Samples of mtDNA were digested with restriction enzymes, electrophoresed in 1.5% agarose gels, and then DNA fragments within the gel were depurinated and transferred to nitrocellulose filters by capillary flow of buffer [20× standard saline citrate (SSC: 0.15 M NaCl, 0.015 M sodium citrate)]. The filters were air-dried, baked in a vacuum oven at 80°C, prehybridized for 1 h, and then hybridized with 1×10^7 cpm of probe in a buffer containing 6× SSC, 40% formamide, and 10% dextran sulfate overnight at 22°C, washed extensively in 2× SSC and then 0.1× SSC at 22°C, and autoradiographed with an intensifying screen for 1–2 days. The low stringency conditions of hybridization and washing were necessary to allow hybrid formation between the primate and dolphin sequences that are significantly diverged and moreover have a high A+T content. After hybridization, washing, and autoradiography, the probe was stripped from the filter by washing at 70°C for 60 min in 0.1× SSC, 0.1% SDS, prior to recycling with the next probe.

Results

Supercoiled mtDNA was purified by density gradient ultracentrifugation from long-term frozen liver tissue of the two dolphin species. Restriction enzyme cleavage maps were established for the two dolphin mt genomes (Fig. 1), and, assuming similar lengths for the two genomes (approximately 16,330 bp), we have used the analytical approach of Nei and Li (1979) to estimate a sequence divergence of 7%. Subsequently, the positions of several specific genes (cytochrome b, cytochrome oxidase subunit II, and D-loop) were determined in both the *C. commersonii* and *D. delphis* mtDNAs by Southern blot analysis using cloned restriction fragments of primate mtDNAs as hybridization probes (Fig. 2).

Restriction fragments, generated by digestion of supercoiled mtDNA from the dolphin *C. commersonii* with the enzymes *Bam*HI or *Eco*RI, were cloned into several vectors including pACYC184, pRK404, pBR322, and Charon 28 and propagated in *Escherichia coli* (Fig. 3). The whole mtDNA, linearized with *Eco*RI, *Bam*HI, or *Hind*III, could not be stably propagated by ligation with any of the vectors. The vectors pBR322 and Charon 28 allowed only stabilization of one *Bam*HI fragment (fragment B, Fig. 3). The stringent, low-copy plasmids pRK404, an R2 derivative (gift of Dr. G. Ditta, Biology Department, University of California, San Diego, La Jolla, California 92093, USA) and pACYC184, a p15A replicon (Fig. 3), appeared to be more suitable for stable recombination with the dolphin mt fragments. Separation of individual mt restriction fragments was necessary to obtain clones of several of the fragments. Similar difficulties were experienced in the isolation of human mtDNA fragments from similar regions (Drouin 1980). The recombinant clones that cover the entire dolphin mt genome are summarized in Fig. 3.

We have determined the nucleotide sequences of several regions of the dolphin mt genome (Fig. 1) using cloned fragments of the *C. commersonii* mtDNA and the chemical sequencing method of

Maxam and Gilbert (1980). The sequenced portions, comprising 2381 bp, contain the entire large noncoding region of 900 bp (Fig. 4), the tRNA^{Thr}, tRNA^{Pro}, and tRNA^{Phe} genes (Fig. 5), partial sequence of the 16S rRNA gene (Fig. 6), and partial sequences of the genes encoding cytochrome b and ND3 (a subunit of the NADH dehydrogenase enzyme complex previously referred to as URF 3, Chomyn et al. 1985) (Fig. 7). The locations and orientations of these genes in the dolphin mt genome are identical to bovine mtDNA (Fig. 1; cf. Anderson et al. 1982).

The dolphin mtDNA sequences were compared with matching sequences from human (Anderson et al. 1981), mouse (Bibb et al. 1981), and cow (Anderson et al. 1982) in order to assess amino acid conservation and the nature and frequency of nucleotide changes. The pattern of amino acid conservation in the dolphin cytochrome b and ND3 proteins (Fig. 7b) is very similar to that in human, cow, and mouse. There is also similarity in the codon usage, and, as in the other mammals, the dolphin cytochrome b translation reading frame ends without a termination codon, which is presumably

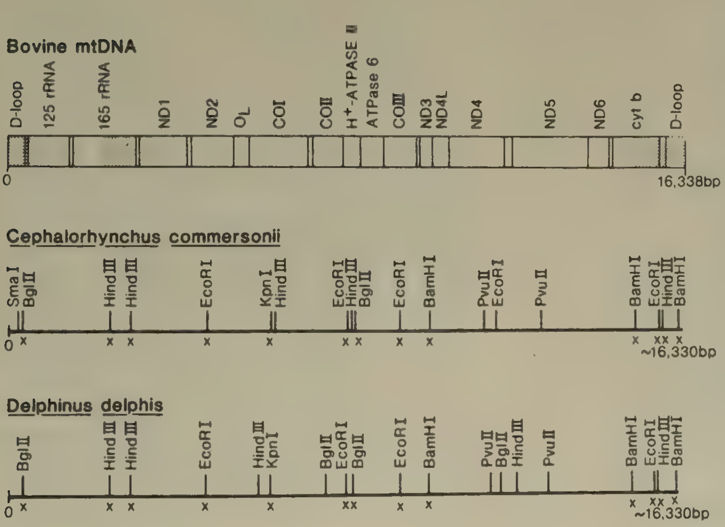
Bovine mtDNA
D-loop
125 rRNA
165 rRNA
ND1
ND2
O_L
COI
COII
H$^+$-ATPASE II
ATPase 6
COIII
ND3
ND4L
ND4
ND5
ND6
cyt b
D-loop
0
16,338bp
Cephalorhynchus commersonii
SmaI
BglII
HindIII
HindIII
EcoRI
KpnI
HindIII
EcoRI
HindIII
BglII
EcoRI
BamHI
PvuII
EcoRI
PvuII
BamHI
EcoRI
HindIII
BamHI
0
~16,330bp
Delphinus delphis
BglII
HindIII
HindIII
EcoRI
HindIII
KpnI
BglII
EcoRI
BglII
EcoRI
BamHI
PvuII
BglII
HindIII
PvuII
BamHI
EcoRI
HindIII
BamHI
0
~16,330bp

Fig. 1. A schematic representation of the dolphin mt genome aligned with bovine mtDNA. Restriction maps of the circular mt genomes from two dolphins, *C. commersonii* and *D. delphis*, are shown in a linear fashion, with the L-strand running 5′ to 3′. Common restriction sites in the two genomes are indicated by x's. The dolphin mt genomes are aligned with the bovine mt genome whose genetic content is shown schematically using conventional abbreviations to indicate coding regions. The order of restriction fragments, orientation of the restriction maps, and similarity of genetic organization between dolphin and cow was verified by genetic mapping and by sequence analysis of dolphin mtDNA. The regions in the *C. commersonii* mtDNA that have been sequenced are indicated by shading of the homologous areas in the bovine mtDNA.

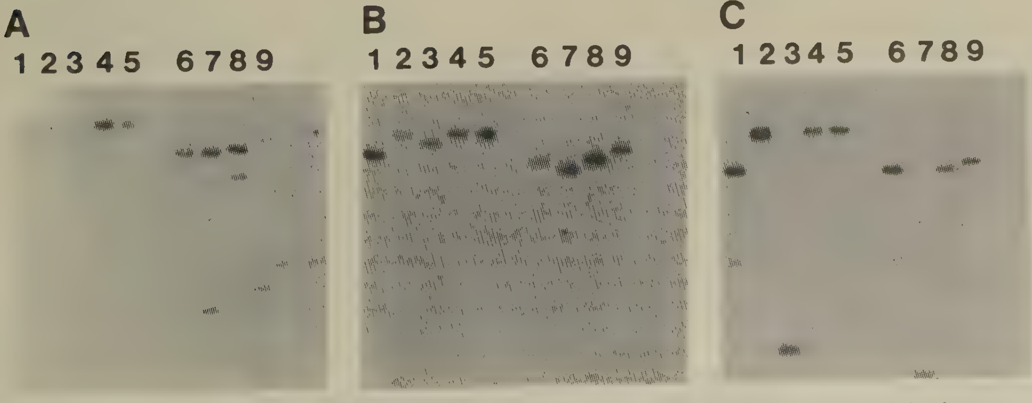
A
1 2 3 4 5 6 7 8 9
B
1 2 3 4 5 6 7 8 9
C
1 2 3 4 5 6 7 8 9

Fig. 2. Mapping of specific genes in mtDNA *D. delphis* using primate mt genes as hybridization probes. Restriction fragments of purified supercoiled mtDNA were generated by single and double digests and separated by gel electrophoresis: lane 1, *Eco*RI; 2, *Bam*HI; 3, *Bgl*II; 4, *Pvu*II; 5, *Kpn*I; 6, *Eco*RI + *Bam*HI; 7, *Eco*RI + *Bgl*II; 8, *Eco*RI + *Pvu*II; 9, *Bam*HI + *Kpn*I. The filter was sequentially hybridized with three different primate mtDNA fragments as genetic probes: A the cytochrome b gene, **B** D-loop, and C the cytochrome oxidase subunit II gene. The precise location of the specific genes in the mtDNA from another dolphin (*C. commersonii*), predicted by the mapping, was subsequently verified by DNA sequencing.

generated by polyadenylation of the transcript (Anderson et al. 1981, 1982; Bibb et al. 1981). The last codon in the dolphin sequence is indicated by an asterisk. The mutation rate of codons increased in the position order: 2, 1, 3. The protein genes appear to evolve by point mutations with preference for changes C–T and A–C (Table 1). The amino acids with the highest positional correlation (Tyr, Phe, Trp, Arg, His, Glu, Gly) include aromatic hydrophobic and charged residues. The amino acids Val, Met, Thr, and Ser are the least conserved ones and seem to be interchangeable in the protein sequence.

The nucleotide sequences of $tRNA^{Thr}$, $tRNA^{Pro}$, and $tRNA^{Phe}$ (Fig. 5a) were compared in schematic cloverleaf configurations allowing assessment of conserved features in the tRNA secondary structure (Fig. 5b). A generalized cloverleaf tRNA structure derived from individual patterns of nucleotide conservation shows considerable variability in the mt tRNA sequences and in the size of single-stranded loops. The position of invariant nucleotides and intrastrand bonds indicates that the most conserved structural features are the anticodon loop, the D.H.U. stem, nucleotides 8 and 9, and the tip of the aminoacyl stem, whereas the T.Ψ.C. loop and the D.H.U. loop appear to be the most variable regions.

The evolution of mt 16S rRNA genes in the compared mammals appears to involve both point mutations with a strong bias toward specific changes C–T, C–A, and A–T, resulting in a high positional conservation of G (Table 1), and length variations similar in size to the rearrangements occurring dur-

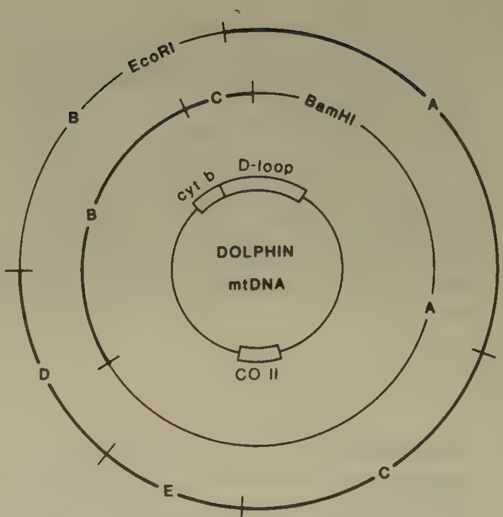

Fig. 3. Summary of recombinant dolphin mtDNA clones in the pACYC184 vector. Restriction fragments generated by digestion of supercoiled mtDNA from the dolphin *C. commersonii* with the enzymes *Bam*HI or *Eco*RI were cloned into the pACYC184 vector. Size-ordered restriction fragments are named in alphabetical order. Available cloned mtDNA fragments are identified by heavy lines. The inner circle indicates the orientation of the dolphin mt genome with the L-strand running 5′ to 3′. We used the mtDNA inserts from the recombinant pACYC184 plasmids to prepare a recombinant dolphin mtDNA probe. Six gel-purified DNA fragments (*Eco*RI: A, C, D, and E and *Bam*HI: B and C) were mixed in approximately equimolar ratios and labeled with α^{32}P-dATP and α^{32}P-dTTP using nick-translation or random primer extension techniques. This recombinant probe hybridized with the entire dolphin mtDNA sequence.

Table 1. Nature and frequency of specific base substitutions in D-loops and the sequences encoding proteins, tRNAs, and 16S rRNAs in mtDNA of dolphin, cow, human, and mouse

Type of change	Protein genes (total number of specific substitutions)[a]		Average bias[b]	tRNA genes (total number of specific substitutions)			Average bias	16S rRNA gene (total number of specific substitutions)	Average bias	Conserved D-loop[c] (total number of specific substitutions)		Average bias
	cyt B	ND3		$tRNA^{Thr}$	$tRNA^{Pro}$	$tRNA^{Phe}$				In blocks A–K	Between blocks B–F	
Transitions												
A ↔ G	47	14	1.33	23	41	17	1.83	95	0.91	19	27	0.75
C ↔ T	120	62	2.25	31	41	37	2.42	169	1.31	59	68	2.07
Transversions												
A ↔ C	103	45	1.83	5	5	15	0.56	155	1.49	24	37	1.04
A ↔ T	32	30	0.77	13	6	11	0.74	144	1.39	29	49	1.27
G ↔ C	14	5	0.23	—	1	—	0.02	28	0.27	11	12	0.37
G ↔ T	12	4	0.20	5	9	3	0.39	34	0.33	13	21	0.55

[a] Substitutions resulting from pairwise comparison of dolphin, bovine, human, and murine mitochondrial sequences as indicated in Table 2

[b] Average bias = 6 × (total number of the specific type of substitutions)/(total number of all types of substitutions). Bias 1.0 represents the case of random frequency of substitutions (probability 1/6)

[c] Conserved sequences in the central region of D-loops (similarity blocks B through F), blocks A, K and H, I, J (when present) were analyzed

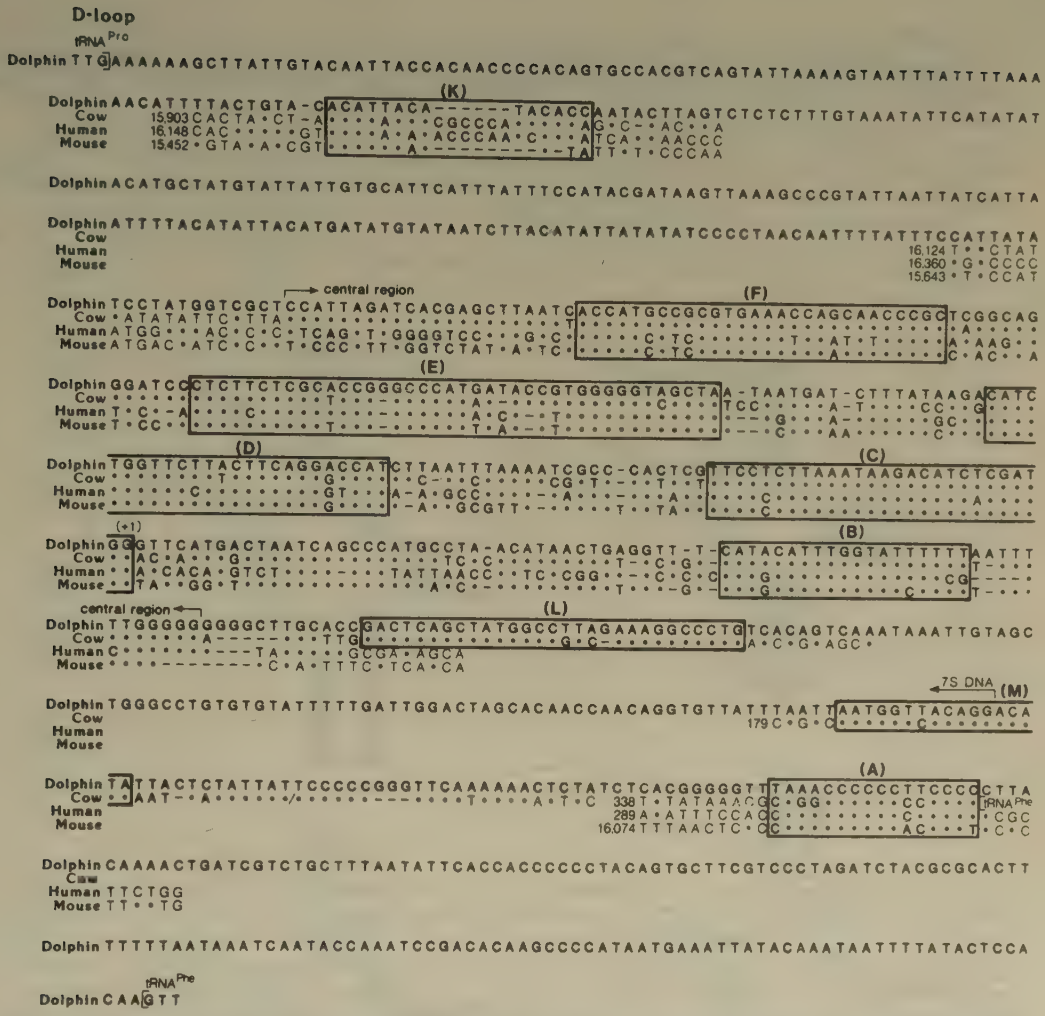

Fig. 4. The nucleotide sequence of the entire dolphin D-loop and the alignment of mammalian mt sequences. The D-loop, comprising 900 bp located between the tRNA^{Pro} and tRNA^{Phe} genes, is shown. The sequence, analogous to the beginning of the published human and bovine mtDNA sequences, is indicated as (+1). Sequence similarity among D-loops of the compared mammals is clustered in a central region of less than 280 bp (marked in the figure) and in the similarity blocks A through M. In addition to the pairwise alignment of the similar sequences, short stretches of adjacent sequences are shown to demonstrate the sharp termination of the clusters of similarity by runs of unique sequences. The start of the bovine 7S DNA is indicated by an arrow; this site has not yet been mapped in the dolphin D-loop. A single deletion of three nucleotides in the bovine sequence (indicated ·/·) has been introduced to maximize the sequence alignment. The mt sequences of the L-strand from the four mammals are aligned to obtain maximum similarity. Positions identical with the dolphin sequence are indicated by dots, and deleted positions and gaps in the sequence, by dashes. In order to facilitate the identification of sequences that have been aligned with the dolphin sequence, nucleotide numbers are included from the published sequences (Anderson et al. 1981, 1982; Bibb et al. 1981).

ing divergence of the mt tRNA genes. Interpretation of the visualized pattern of the structural conservation has to await elucidation of the mt 16S rRNA structure.

Information derived from this comparative analysis of dolphin mt genes shows that the degree of sequence similarity between dolphin and cow is higher than for any other pair of mammals that have been compared at both the nucleotide and amino acid levels (Table 2).

Comparison of D-loop regions of human, cow, and mouse provided information on the presence

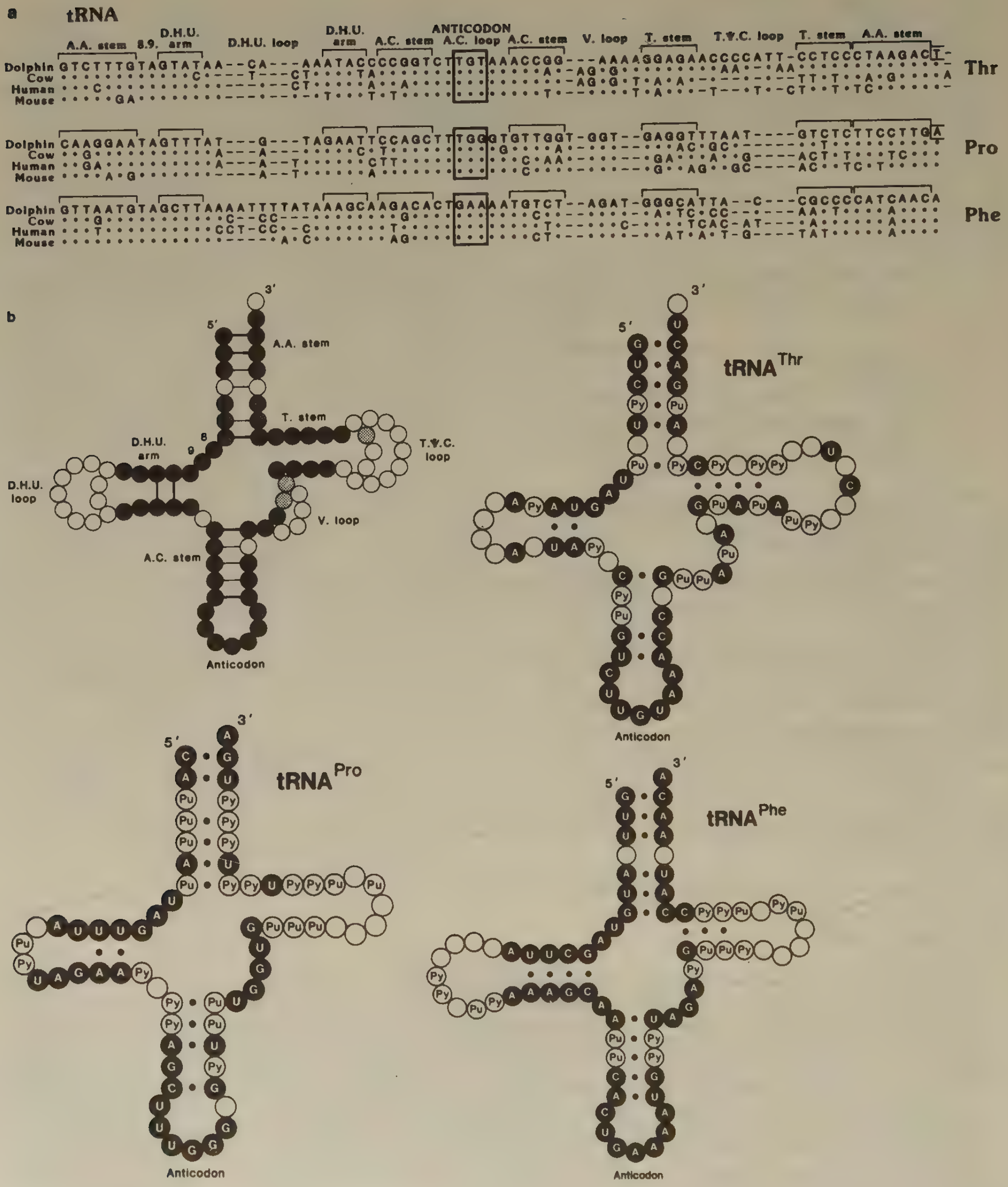
a
tRNA
A.A. stem
8.9.
D.H.U. arm
D.H.U. loop
D.H.U. arm
A.C. stem
ANTICODON
A.C. loop
A.C. stem
V. loop
T. stem
T.Ψ.C. loop
T. stem
A.A. stem
Dolphin
Cow
Human
Mouse
Thr
Pro
Phe
b
3'
5'
A.A. stem
T. stem
D.H.U. arm
8
9
D.H.U. loop
T.Ψ.C. loop
V. loop
A.C. stem
Anticodon
tRNA^Thr
tRNA^Pro
tRNA^Phe

Fig. 5. Sequences of mt tRNA^{Thr}, tRNA^{Pro}, and tRNA^{Phe} genes. **a** The three tRNA genes are shown in a pairwise alignment with other mammalian mt sequences (as in Fig. 4) and also aligned with each other vertically to demonstrate the similarity between the mt tRNAs and the classical tRNA structure, whose various loops and stems are marked by conventional abbreviations along the top of the figure. The anticodon triplets are enclosed in boxes. **b** The tRNA sequences also are compared in schematic cloverleaf configurations to allow assessment of secondary structure conservation. The sequences of the dolphin tRNA^{Thr} and tRNA^{Pro} genes overlap for the terminal nucleotide (indicated in the figure). A composite tRNA structure has been derived from the individual 12 sequences in order to visualize the consensus pattern of structural conservation in the mt tRNA. The degree of conservation of the individual nucleotide positions and the base-pairing pattern are indicated by color intensity of the symbols representing bases and intrastrand bonds. A black circle represents a fully conserved nucleotide, whereas a white circle indicates that the position can be occupied by any nucleotide. In order to indicate variability in the D.H.U. and T.Ψ.C. loops, all alternative loop sizes are shown.

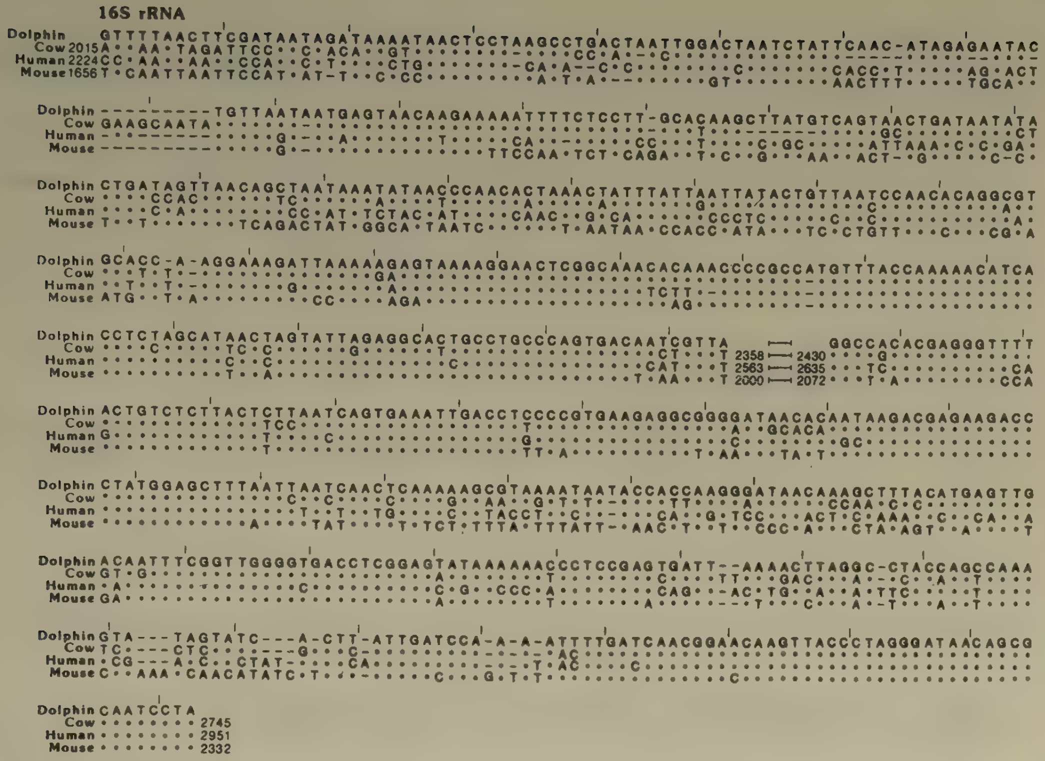

Fig. 6. Comparisons of sequences from mt 16S rRNA genes. The mammalian mt sequences are aligned as described in Fig. 4.

of several clusters of conserved sequences, referred to as similarity blocks A through K, in an otherwise highly divergent sequence (Anderson et al. 1982). The dolphin D-loop region, comprising 900 bp (Fig. 4), is very similar in size to that of the cow (910 bp, Anderson et al. 1982). However, the patterns of similarity blocks in dolphin and cow are different (Fig. 8), and the bulk of the dolphin D-loop sequence is unique. The middle of the D-loop, covered by the 7S DNA, was shown to be the most conservative region in D-loops of human (Anderson et al. 1981), cow (Anderson et al. 1982), goats and sheep (Upholt and Dawid 1977), mouse (Bibb et al. 1981), and rat (Sekiya et al. 1980), and appears to be well conserved also in dolphin. This central D-loop region (Figs. 4 and 8), spanning less than 300 bp, contains a compound group of five similarity blocks (B, C, D, E, F) with extremely high sequence conservation in all four mammals (85–96%, Table 2). These central blocks of similarity are separated by short segments of variable length and sequence (40–56% sequence conservation). In contrast, dolphin and cow show very high similarity throughout the entire central region (the interblock sequences are 70% conserved) and beyond. We identified two similar sequences, termed blocks L and M (83% and 94% conserved), that are present only in dolphin and cow (Figs. 4 and 8). In cow, the block M spans the putative start of bovine 7S DNA. Two additional blocks of similarity shared by all four mammals, A and K, are less conserved than the central blocks (79% and 58%), and they are flanked by long stretches of highly divergent sequences. The blocks G, H, and J are absent from the dolphin D-loop (Fig. 8), but their sequences are highly conserved when present in other mammals (Anderson et al. 1981, 1982; Bibb et al. 1981). Except for the 13 blocks of sequence similarity and the conserved compound structure of the central region, up to 70% of the D-loop sequences in dolphin and other mammals are unique.

Discussion

The sequence comparisons of dolphin, bovine, human, and murine mt genes presented here confirm

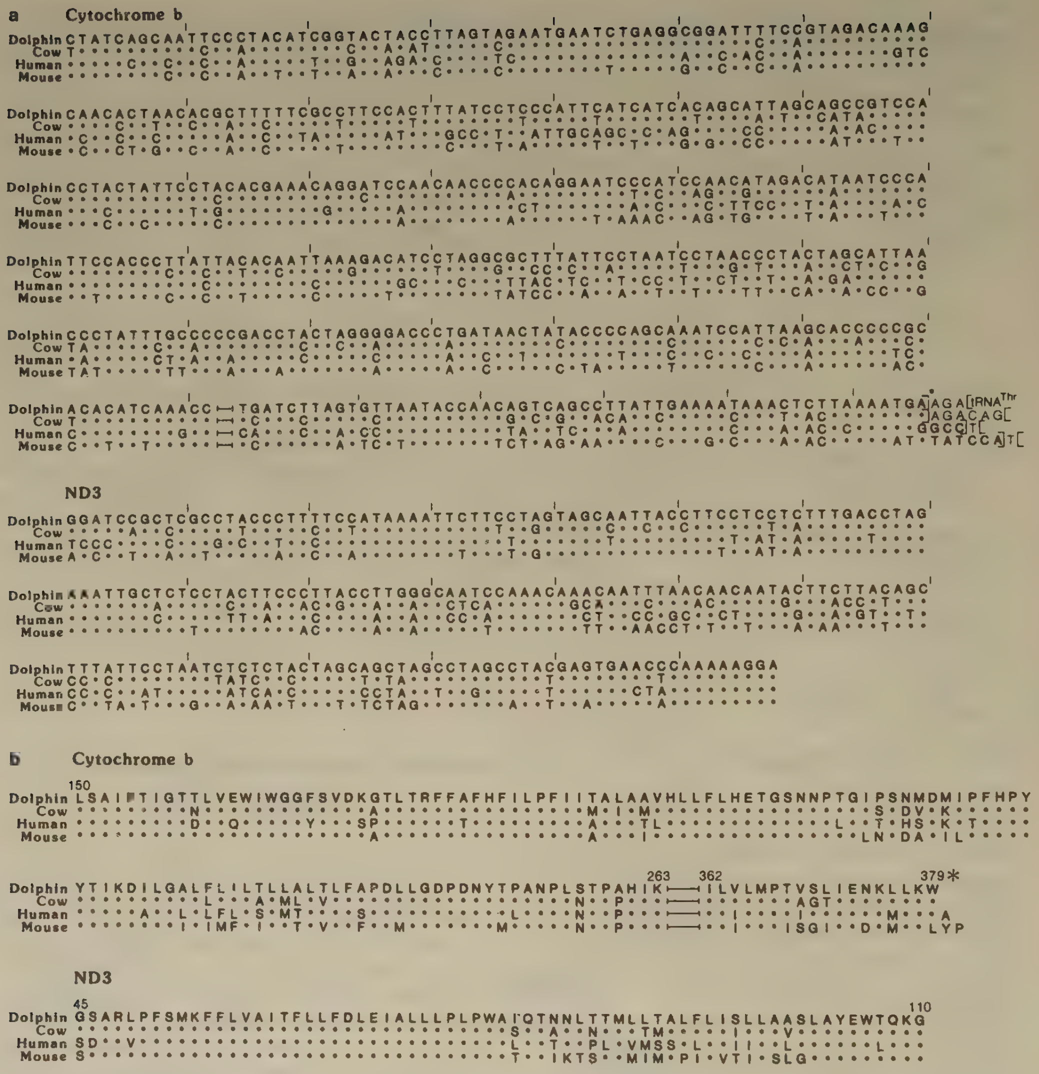

Fig. 7. Comparisons of sequences from mt proteins cytochrome b and ND3. Both the nucleotide sequences of the protein genes (a) and the inferred amino acid sequences (b) are compared with other published mt sequences. The sequences are aligned as described in Fig. 4.

that the mammalian mt genome has not evolved in the same way and at the same rate in all regions. Several distinct mechanisms seem to contribute to mtDNA variability. Evolution by point mutation has occurred throughout the genome, although there are differences in the probabilities of specific types of nucleotide changes (Table 1). This gene-specific pattern of nucleotide substitutions probably reflects functional constraints on the products of these genes and on the thermodynamic stability of mtDNA conformations. Point mutations are the principal mechanism for divergence of the protein genes, whereas sequence changes in the tRNA and rRNA genes also involve short insertions and deletions. Large sequence rearrangements including recombination events appear to occur in the D-loop region, which is the most dynamically evolving portion of the mt genome.

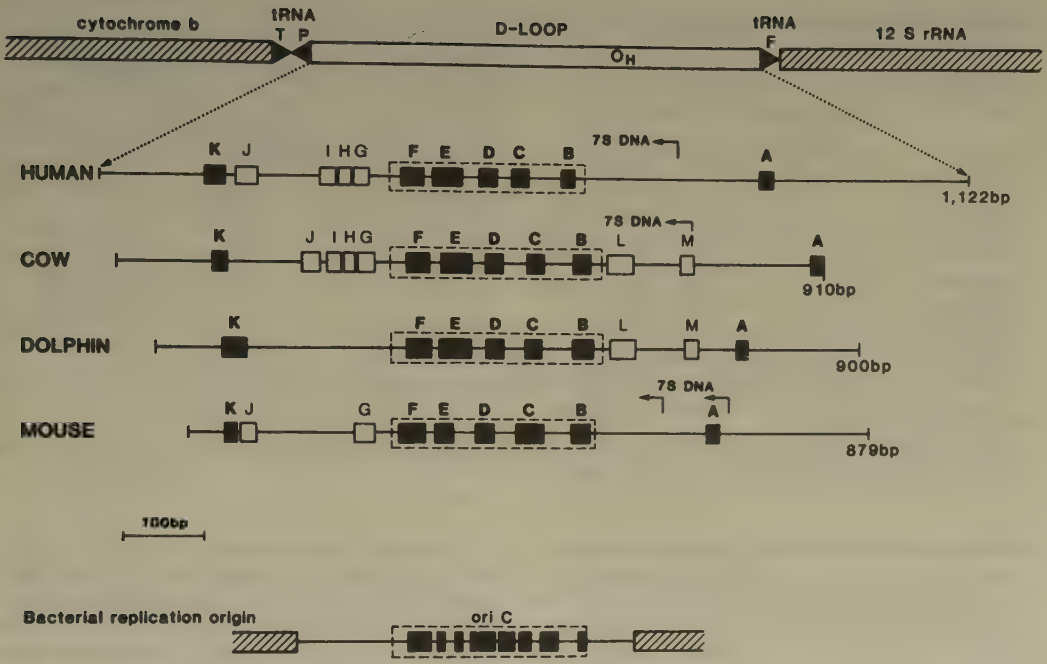

Fig. 8. Generalized pattern of sequence similarities in mammalian mt D-loops and possible relations to bacterial *ori*C. The mammalian D-loops are aligned using the sequence similarity (see Fig. 4) of a highly conserved central region (enclosed by a dashed line). Similarity blocks present in all mammalian D-loops examined (Anderson et al. 1981, 1982; Bibb et al. 1981) are represented by shaded boxes, whereas blocks only present in some mammals are shown by open boxes. Length variation within the D-loop arises from unique sequences that alter the relative position of some similarity blocks with respect to the central region and the tRNA genes designating the extremities of the D-loop region. The origin of DNA replication for the H chain is represented by O_H. The mapped starting positions of 7S DNAs, associated with H-chain replication, are shown by arrows. The 245-bp minimal bacterial origin of chromosomal replication (*ori*C, enclosed in a dashed box) contains short blocks of conserved sequence, which are present in six species of enterobacteria (Zyskind et al. 1983).

The additive effect of various mutational events results in different characteristics and rates of sequence change in distinct functional regions of the mt genome. Consequently, only a complex statistical representation that considers regions with different modes of evolution separately would appear to be appropriate for analysis of mtDNA divergence.

Considering possible relationships between DNA structure and function, it is interesting to note a similarity between the mt D-loop regions (Fig. 8) containing regulatory signals for mtDNA replication (Anderson et al. 1981, 1982; Bibb et al. 1981) and the bacterial chromosomal replication origin, *ori*C (Zyskind et al. 1983). The consensus structures of the D-loop and *ori*C both consist of interspersed blocks of conserved sequences (Fig. 8). These bacterial similarity blocks are not related by sequence to the mt blocks, but the general organization of *ori*C resembles the mt D-loop. this may reflect the prokaryotic origin of the mt genetic system (the endosymbiotic hypothesis), or the pattern of interspersed conserved and variable sequences may represent an efficient structural organization of a genomic replication origin that has evolved independently in separate genetic systems.

High sequence conservation in the similarity blocks of the D-loop region may indicate functional importance (Anderson et al. 1982); however, the absence of the blocks G, H, I, J, L, and M in several of the examined mammals (Fig. 8) poses questions about the nature of their function in the other mt genomes. It appears that while several of the similarity blocks may form a group of invariant sites present in all mammals and be crucial for the regulatory functions encoded in D-loops, other blocks, conserved only in certain species, may be involved in more specialized functions.

Although a certain degree of functional conservation can be inferred from the patterns of similarity blocks discussed above, we suggest that the D-loop has additional invariant features that are not apparent by direct comparisons of linear sequences but

Table 2. Similarity of mitochondrial genes in dolphin, cow, human, and mouse[a]

Species compared	Protein genes[b]				tRNA genes[c] nucleotide similarity (%)			16S rRNA[d] nucleotide similarity (%)	D-loop[e] nucleotide similarity (%)		
	Nucleotide similarity (%)		Amino acid similarity (%)						Within blocks B–F	Between blocks B–F	Unique sequences
	Cyt b	ND3	Cyt b	ND3	tRNA$^{\mathrm{Thr}}$	tRNA$^{\mathrm{Pro}}$	tRNA$^{\mathrm{Phe}}$				
Dolphin, cow	79	79	86	88	77	79	73	81	96	77	26
Dolphin, human	70	70	78	76	68	63	71	74	86	43	31
Dolphin, mouse	72	73	78	74	67	72	71	69	90	56	20
Cow, human	69	73	78	77	68	65	71	70	88	40	22
Cow, mouse	77	73	80	76	63	60	70	66	90	53	28
Human, mouse	69	70	74	71	67	66	69	66	90	42	33

[a] Data on human, bovine, and murine mtDNA sequences were published previously

[b] Cytochrome b, 414 bp (138 codons) compared; ND3, 198 bp (66 codons) compared

[c] Dolphin tRNA$^{\mathrm{Thr}}$, 71 bp; tRNA$^{\mathrm{Pro}}$, 67 bp; tRNA$^{\mathrm{Phe}}$, 72 bp

[d] 16S rRNA, 657 bp compared

[e] Central region of D-loop, comprising 263 bp and containing blocks of similarity B through F, was compared (Figs. 2 and 3) and 100 bp in the unique sequences flanking the central region

can be surmised by analysis of conformational properties (Brown et al. 1986) and physicochemical profiles (Mignotte et al. 1987) of animal D-loops. The less-apparent features involve local thermodynamical, stereochemical, and topological properties of the DNA molecule (Lukesová-Southern 1982). Distribution of the collective physicochemical properties within the D-loop determines the dynamic profile of the region: potential for occurrence of local changes in DNA conformation (confined to within 100 Å or 10–40 bp of linear sequence) such as B- to Z-DNA transition, strand separation, and formation of a gap or a hairpin loop. These localized and transient molecular deformations in supercoiled mtDNA constitute reactive sites with distinct stereochemical properties, which could participate in protein–DNA interactions or in formation of multistrand DNA structures (Lukesová-Southern 1982). Such molecular interactions in D-loops were proposed to be required in the process of transcription and replication of the mt genome, and therefore the physicochemical properties of D-loop DNA, which are necessary for these interactions, are likely to be conserved in evolution.

Our results establish a strong similarity between dolphin and bovine mtDNA sequences. The suggestion of a close evolutionary relationship between cetaceans and ungulates is consistent with current theory on cetacean origin (Barnes et al. 1985), inferred from biochemical, anatomical, and physiological comparisons of modern mammals and the fossil record relating to cetacean phylogeny (Gingerich et al. 1983). However, appropriate statistical analyses of mtDNA sequences from different cetacean and ungulate taxa are needed for an accurate assessment of the early evolution of dolphins and whales.

Addendum. In a related study, we (A.E.D., S.O.S., and others, manuscript in preparation) have used a mixture of recombinant mtDNA fragments as a hybridization probe to determine mtDNA genetic distances among and within species, populations, and schools of spinner and spotted dolphins. When supercoiled mtDNA, purified from frozen tissues, was used as a hybridization probe against total cell DNA, various nonspecific and satellite nuclear DNA fragments were often detected due to their copurification with mtDNA. The recombinant dolphin mtDNA probes have eliminated these problems.

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Index Numbers and Productivity Measurement in Multispecies Fisheries: An Application to the Pacific Coast Trawl Fleet

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ABSTRACT

This study is concerned with the measurement of total factor productivity in the marine fishing industries in general and in the Pacific coast trawl fishery in particular. The study is divided into two parts. Part I contains suitable empirical and introductory theoretical material for the examination of productivity in the Pacific coast trawl fleet. It is self-contained, and contains the basic formulae, empirical results, and discussion. Because the economic theory of index numbers and productivity is constantly evolving and is widely scattered throughout the economics literature, Part II draws together the theoretical literature into one place to allow ready access for readers interested in more details.

The major methodological focus of the study is upon the type of economic index number that is most appropriate for use by economists with the National Marine Fisheries Service. This study recommends that the following types of economic index numbers be used: chain rather than fixed base; bilateral rather than multilateral; one of the class of superlative indices, such as the Tornqvist or Fisher Ideal.

PART 1

Introduction

Purpose of study

Measurement of industry productivity is important to planning, public regulation, and monitoring industry performance over time. Yet, with the exceptions of Bell and Kinoshita (1973), Norton et al. (1985), Kirkley (1984), and Duncan (undated), little attention has been given to measuring productivity in marine fishing industries. Moreover, these initial studies can be extended in scope and methodology to draw upon recent advances in the economic theory of index numbers and productivity measurement.

This study addresses these issues and has five explicit purposes. First, the study applies recent advances in the theory of index numbers to the Pacific coast trawl fleet. Second, an informal evaluation is made of the data sources available for productivity measurement of this fleet. Third, many different index-number procedures are available, and this study evaluates the most important and widely used procedures. Fourth, the interpretation of productivity is unclear for marine fishing industries, and this study clarifies this issue. Fifth, the economic theory of index numbers is constantly evolving and is widely scattered throughout the literature. This study draws this literature together to make it more accessible to other applied economists.

The productivity indices are developed for U.S. vessels of the Pacific coast trawl fleet homeported in Washington, Oregon, and northern and central California over the 1981-85 period. These vessels employ bottom, shrimp, and midwater trawl gear to harvest numerous species of groundfish and pink shrimp which are sold to domestic shoreside processors or to foreign processors participating in joint venture operations.

Applications of productivity measures

Productivity measures, used as indicators of relative economic performance in fisheries, portray fishery trends and problems. Productivity measures can be an effective means to monitor the economic performance of a fishery. Only by accurate knowledge of a fleet's performance over time can effective policies be designed. For example, declines in fleet productivity could signal a need for government assistance or regulation. Alternatively, productivity declines after years of government assistance could imply that public resources committed to the fishery have been dissipated through overcapitalization. Government support might be either scaled back or refocused to foster efficiency without encouraging increases in input usage. If public regulation of fisheries is to be concerned with net economic and social benefits, regulators should be aware of changes in productivity and in resource stock levels.

Small or negative productivity gains in fishing industries can be associated with lagging profits, returns to labor, and employment, because fishermen must compete with foreign fishery imports and other protein substitutes, such as meat and poultry, where productivity is a main component of competitive advantage. Rising productivity in the fishery sector can also help mitigate inflationary pressures in fish products, because products can be supplied at declining costs over time. In turn, this helps to maintain the competitive capability of fisheries in relationship with its close substitutes such as meat and poultry (Bell and Kinoshita 1973).

International comparisons of fishing fleet productivity can help clarify differences in international competitiveness of fishing industries. Decline in a fishery's productivity coupled with rising imports of the species being harvested could suggest a need for corrective action by industry bodies or government. Declines in productivity coupled with a structural shift in consumption patterns toward more fish could signal an increase in imports or a decrease in exports in the future.

Regional differences in productivity can be linked to the geographical distribution of productive resources within the fishery. For example, the empirical results presented later in this report show that in 1983 trawl fleet capital declined in Washington while it increased in northern and central California. Moreover, Washington and Oregon experienced positive growth rates in fleet total-factor productivity over the time period 1981-85, while northern and central California experienced declines. Public regulation might become more effective by adopting a more explicitly regional-based approach.

The Pacific trawl fleet

The Pacific trawl industry off California, Oregon, and Washington is composed of several different commercial gear and vessel types harvesting a wide array of species. The most important harvested species include pink shrimp, Dungeness crab, flatfish (Dover, English, petrale, rock, and rex sole), roundfish (sablefish, Pacific cod, ling cod, and Pacific whiting), the Sebastes complex (yellowtail, canary, widow, boccacio, chillipepper, and shortbelly rockfish), and thornyheads.

The contributions of each species and species assemblage to total revenue are provided in Table 16. This table shows the proportions or shares of total regional exvessel revenue received for each species assemblage in each year. Pink shrimp, rockfish, and Dover sole consistently provide the highest proportion or share of total revenue. The contributions of each region to total revenue, or revenue shares, are reported in Table 17. Oregon generally provides about 45% of the total revenue, Washington around 22%, northern California around 20%, and central California the balance. The species' and regions' revenue shares are not static, but change over time.

Three separate trawl fisheries exist for pink shrimp, groundfish, and midwater species. Gear switching occurs, most notably between otter and shrimp trawls and between otter and midwater trawls. Huppert and Korson (1987) note that smaller inshore trawlers in the Crescent City, California, area also shift among target species by harvesting Dungeness crab in the winter and otter trawling for soles and rockfish during the fall and spring. The midwater trawl fishery harvests Pacific whiting in joint ventures and widow rockfish for shoreside landings. For a brief period in 1982, midwater trawlers caught shortbelly rockfish. Many vessels that participate in the pink shrimp and groundfish fisheries have insufficient horsepower to operate the midwater trawls.

Increased profits and the availability of vessel financing led to a significant expansion of the shrimp fishery in the late 1970s (Dewees 1986). Since the early 1980s, however, the shrimp fishery steadily declined in importance, dropping from 19,923 short tons worth $20 million in 1981 to 4,814 short tons worth $3.81 million in 1984. A resurgence began in 1985, with landings rising to 12,779 short tons worth $7.61 million (all dollars are $1981 values) (Table 1). The contribution of shrimp to regional exvessel revenue declined from 36% and 46% of total 1981 revenue in Washington and Oregon, respectively, to 13% and 9% in 1984, before rebounding to 29% and 22% in 1985 (Table 16).

During the early 1980s, the groundfish fishery continued the expansion begun following the Magnuson Fisheries Conservation and Management Act of 1976. Table 2 indicates the number of coastwide otter and shrimp trawl vessels in the fishery between 1981 and 1985. Some of the otter trawl vessels were formerly pink shrimp trawlers that switched to otter trawling after the decline in pink shrimp catches and abundance. The decline in the number of otter trawl vessels during 1983 and 1984 can be attributed, in part, to declining rockfish stocks (particularly widow rockfish), continual decline in real groundfish prices, and the effects of high interest loans taken out to finance the fleet's expansion. Some of the larger vessels transferred their operations to Alaska, while other vessels have sunk, burned, been repossessed, transferred to other fisheries, or simply tied up due to financial difficulties.

Otter-trawl groundfish landings in Washington, Oregon, and northern and central California during the 1980s have declined from a 1982 peak of 113,492 short tons valued at $44.33 million (1981 constant dollars) to 79,938 short tons worth $32.26 million in 1984, before increasing slightly in 1985 to 82,988 short tons worth $34.86 million (Table 1). Although the number of vessels, tonnage landed, and total revenue all peaked in 1982, the total frequency of landings (i.e., the number of fish receipts recorded) reached a high one year later, with 15,436 landings (Table 4).

The midwater trawl fishery developed in the late 1970s as joint ventures (JV) with foreign fishing companies. With the exception of limited fishing for shortbelly rockfish in 1982, the joint-venture fishery targets Pacific whiting almost exclusively. This fishery occurs primarily in the summer months. Additional sources of revenue for these vessels include widow rockfish and JV operations in Alaska. Annual landings and revenue by Pacific whiting JV vessels were stable during 1982-85 at around 80,000 short tons valued at around $10 million ($1981 dollars) before declining in 1985 to 34,934 short tons worth $3.2 million (Table 1).

The Pacific trawl fleet has undergone a rapid modernization since 1976. Dewees (1986) examines the rates of adoption of eight technological innovations during this period. The innovations ostensibly contributing most to increases in the technical capabilities (or "fishing power") of trawlers have been the development of midwater trawling, chromoscopes, sonar, and track plotters. Midwater trawling represents a major change in the harvesting process. Midwater trawlers have shown a greater reliance on these electronics since otter trawlers can still function satisfactorily without them.

With other factors affecting productivity held constant, these technological innovations should increase productivity in the Pacific trawl industry. Benefits from technological progress can be realized, however, only if productivity gains are not dissipated through overcapitalization in the fishery. Moreover, the rate of technical progress should be comparatively high in open-access fisheries because of the intense competition among fishermen to harvest limited fish stocks.

In recent years, most of the commercial groundfish stocks have been harvested at or near the maximum sustainable yields (MSY) estimated by the Pacific Fishery Management Council's Groundfish Management Team. Dover sole, Petrale sole, other flatfish, Canary, yellowtail, and widow rockfish, ling cod, Pacific ocean perch, and sablefish in particular are all harvested at levels close to, or surpassing, MSY (PFMC 1985; Huppert and Korson 1987). The Pacific whiting catch remains well below its estimated MSY. The pink shrimp resource is somewhat ephemeral and receives intensive exploitation (Korson 1984).

Changes in resource abundance and composition will affect productivity in marine harvesting industries. With the fishery stocks being harvested at levels close to or at their MSYs in the Pacific coast trawl fisheries, economic index measures of fleet productivity are likely to remain unchanged or exhibit downward movements over 1981-85, reflecting constant or declining levels of stock abundance.

Methodological background

This section provides an introduction to the methodology of productivity measurement and the theory of economic index numbers. Productivity is first defined, then the concept of economic index numbers is discussed, followed by discussions of different index-number formulae, chain and fixed-base indices, and bilateral and multilateral indices. Readers interested in additional methodological issues can refer to Part 2 and its Appendices.

Productivity defined

Productivity is traditionally used to explain the physical output per unit of input. Higher productivity means that more can be produced with the same bundle of inputs or, conversely, that the same output bundle can be produced from fewer inputs.

Historically, productivity measurement focused upon one factor, such as output per unit of capital or output per man-hour (Bell and Kinoshita 1973). These partial productivity measures may provide misleading results, since output increases may arise from the increased use of other inputs or changes in capacity utilization. This limitation to partial productivity has led to emphasis upon total-factor productivity.

Dividing the level of production (total output) by an index of all inputs creates an index of total-factor productivity. Properly constructed, the total-factor productivity index accounts for all changes in the quantities of inputs. Variation in the total-factor productivity index tracks the productivity residual which is not accounted for by changes in the volume of economic inputs. With this introduction, the concept of total-factor productivity is now rigorously developed.

Growth-accounting framework

The standard framework for estimating productivity change is derived from the theory of production. Consider the following one output-two input production function:

$$Y(t) = A(t)f[K(t), L(t)], \qquad (1)$$

where $Y(t)$ denotes total landings at time t, $K(t)$ denotes the flow of capital services at time t, $L(t)$ is the flow of labor services used at time t, and $A(t)$ is an efficiency parameter allowing for shifts in the production function. The production function defines the maximum output achievable with the given quantity of inputs, $L(t)$ and $K(t)$, and is determined by the state of technical knowledge and resource abundance, $A(t)$. Total landings can grow from several sources: (1) as existing firms expand their input usage, (2) as new firms enter the industry, and (3) as technology advances and resource abundance increases, causing shifts in the aggregate production function.

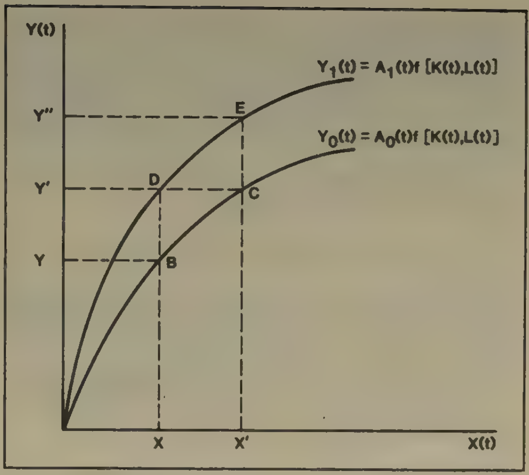

Figure 1
Production function representation of total-factor productivity.

Intuition into the meaning of productivity is provided by Figure 1. Two different levels of the production function in equation (1) are presented: $Y_0(t) = A_0(t)f[K(t),L(t)]$ and $Y_1(t) = A_1(t)f[K(t),L(t)]$, where $Y_1(t) > Y_0(t)$. The vertical axis represents different catch or output levels, where $Y' > Y$. The horizontal axis represents different levels of an index of aggregate input, X, where $X' > X$. When the state of technical knowledge and resource abundance both remain constant but a larger quantity of inputs is used to harvest fish, $X' > X$, and firms move along the existing production function, $Y_0(t) = A_0(t)f[K(t),L(t)]$, from point B to point C. Firms harvest more fish by using more capital and labor, and total catch increases from $Y(t)$ to $Y'(t)$. Total catch can also increase when technological innovations are adopted by the fleet, even if the same amount of inputs is used and resource abundance remains constant. In this case, the state-of-technology index increases from A_0 to A_1, and the production function shifts from $Y_0(t) = A_0(t)f[K(t),L(t)]$ to $Y_1(t) = A_1(t)f[K(t),L(t)]$. At a constant input bundle X, the shift upwards of the production function is denoted by moving from point B to point D and catch increases from Y to Y'. Fishing firms can now harvest a larger catch, Y', with the same level of inputs, X. Economists say that fishing firms are now more productive.

The basic problem of productivity analysis is to use data on the prices and quantities of inputs and outputs to allocate the growth of $Y(t)$ among the growth rates of $K(t)$, $L(t)$, and $A(t)$. The growth-accounting framework used in this study proceeds nonparametrically by first taking logarthims of equation (1) and then logarithmically differentiating equation (1) with respect to time. The logarithmic differential of (1) can be written as:

$$\begin{aligned} d\ln Y(t)/dt &= (dY/dt)(1/Y) \qquad (2) \\ &= [\partial \ln Y(t)/\partial \ln K(t)]\ [d\ln K(t)/dt] \\ &+ [\partial \ln Y(t)/\partial \ln L(t)]\ [d\ln L(t)/dt] \\ &+ [\partial \ln Y(t)/\partial \ln A(t)]\ [d\ln A(t)/dt] \end{aligned}$$

where $\partial \ln Y(t)/\partial \ln A(t)$ is set equal to unity because it is a technology-shift parameter, $\partial \ln Y(t)/\partial \ln K(t) = [\partial Y/\partial K]\,[K/Y]$ is the output elasticity for capital (the percentage increase in output with a 1 percent increase in capital), denoted E_K, and $\partial \ln Y(t)/\partial \ln L(t) = [\partial Y/\partial L]\,[L/Y]$ is the output elasticity for labor (the percentage increase in output with a 1 percent increase in labor), denoted E_L.

The logarithmic derivatives are interpreted as rates of growth so that the rate of output growth becomes:

$$Y(*)/Y = E_K K(*)/K + E_L L(*)/L + A(*)/A, \qquad (3)$$

where the asterisk * denotes time derivatives. The rate of output growth is thus allocated among growth in capital and labor, technical progress, and changes in resource abundance.

Because E_K and E_L are unobservable, equation (3) cannot be used for empirical analysis. One further step is required. Assuming that inputs are paid their value of marginal product:

$$\partial Y(t)/\partial K(t) = P^K(t)/P(t),\ \partial Y(t)/\partial L(t) = P^L(t)/P(t), \qquad (4)$$

where $P(t)$, $P^K(t)$, and $P^L(t)$ are the prices of output, capital services (rental price), and labor services (wage rate), respectively. Substituting (4) into (3) gives:

$$Y(*)/Y = S_K K(*)/K + S^L L(*)/L + A(*)/A. \qquad (5)$$

Because in competitive open-access equilibrium, industry profits are dissipated (Gordon 1954) and firms display locally constant returns to scale (Baumol et al. 1982), total costs equal total revenue, and any input's cost share equals its revenue (or income) share. Therefore, $S_K = [P^K K]/[PY]$ and $S_L = [P^L L]/[PY]$, that is, the cost (equals revenue) shares of capital and labor. Given (3), these shares are equal to the production elasticities E_K and E_L. These shares provide weights to the growth of capital and labor over time.

The final step is to rearrange equation (5) to give:

$$A(*)/A = Y(*)/Y - S_K K(*)/K - S_L L(*)/L. \qquad (6)$$

Productivity in fisheries, that is, technical progress and change in resource abundance, is therefore measured as the residual of output growth after accounting for the growth of inputs. Intuitively, output grows over time as inputs increase and is reflected in movement along the frontier of the industry production function, while technical progress and changes in resource abundance cause shifts in the production function. The residual (6) thus is a measure of production function shift, and is called the productivity residual.

Tracking the total-factor productivity index for a fishing industry therefore provides information on technical progress and changes in resource abundance of exploited fish stocks. Because the productivity index is measured as a residual in equation (6), changes in productivity might also include changes in the economic efficiency of the individual fishing firms, altered fishing regulations, variations in economic capacity utilization, or variations in exogenous conditions like weather.

The effects of changing resource abundance can be disentangled from the productivity residual. This topic is the subject of current research, and will be discussed in a future report.

After defining and clarifying the issue of productivity in marine fishing industries, attention must be turned to measuring productivity in some way. Economic index numbers have been developed by economists for tasks such as productivity measurement. The next section provides a brief introduction and survey of this important topic, while readers interested in additional details can refer to Part 2.

Economic index numbers

Productivity, production, and input use are more effectively measured by economic index numbers than by physical measures. Physical measures (e.g., total catch per hour towed) fail to distinguish changes or differences in composition or quality over time and space, or between fishing firms. Simply lumping together total tonnage of catch in one time period and comparing with total tonnage from a subsequent time period neglects the change in catch composition. Different products are then compared, and the assumption is implicitly maintained that a ton of Pacific whiting, for instance, is perfectly substitutable by a ton of pink shrimp.

Economic index numbers deal with situations in which industry outputs and inputs are too diverse to measure simply by weighing or counting. Economic index numbers provide weighted measures of the different kinds of outputs (species) or inputs (capital, labor, fuel). Shares or proportions of total revenue (revenue shares), for example, can be employed to combine the different outputs into a weighted measure of total output, and shares of total costs (cost shares) can similarly be employed to aggregate different inputs into a weighted measure of total input.

The different outputs (inputs) are combined into weighted measures of total output (input) by functions. These functions are called aggregator functions since they aggregate the individual components (e.g., outputs) into the composite (e.g., total output). Different formulae for the aggregator functions have different implications for the properties of the index numbers formed. The economic theory of index numbers is concerned with these relationships between the properties of index numbers and the properties of the underlying aggregator functions they represent.

Both individual quantities and individual prices can be aggregated into a composite quantity or price. Quantity aggregator functions aggregate quantities of individual outputs or inputs into composite measures of total-output quantity or total-input quantity, while price aggregator functions aggregate prices of individual outputs or inputs into composite measures of total output or input prices.

Index-number formulae

A number of different types of economic indices exist. Each type of index offers an approximate scalar measure of a multidimensional change over time in prices, quantities, or productivity. The different indices approximate these intertemporal changes in different ways, according to their theoretical properties (manifested by their formulae). Differences in indices can be viewed as differences in their abilities to provide approximations to the intertemporal changes in prices, quantities, or productivity.

Consider a concrete example of the way in which the different indices provide different approximate scalar measures of intertemporal changes. Suppose the problem is to measure intertemporal changes in an aggregate output bundle, which in fisheries is the change in total catch over time. One of the most important issues in constructing an economic index number for cases such as these is to account for intertemporal changes in the relative composition of this bundle, that is, the changes in species mix. When output (species) prices change relative to one another, fishermen alter the individual species (output) composition of their catch (aggregate output). An index number that does not properly incorporate these intertemporal changes in output composition into the aggregate measure becomes increasingly biased over time, that is, the errors in approximation increase.

The different index numbers approximate changes such as these in different ways, and thus have different degrees of accuracy. When intertemporal changes (in productivity or output and input prices and quantities) are relatively small, the different indices all provide reasonably accurate and similar approximate scalar measures of these changes. Typically, the larger the changes over time, the more the measures from different indices diverge from one another. This departure occurs because the indices provide approximations in differing ways.

Four economic index numbers are commonly applied: Laspeyres, Paasche, Tornqvist, and Fisher Ideal. These indices correspond to different methods of approximation (reflected in the formulae of their aggregator functions) with correspondingly different properties. The Laspeyres and Paasche indices have tradionally been widely applied, but the Tornqvist and Fisher Ideal are increasingly used.

Laspeyres and Paasche indices—The Laspeyres and Paasche indices are the most widely used. In forming aggregates, these indices weight individual outputs or inputs with prices or quantities. The Laspeyres index for quantities of inputs or outputs may be written:

$$Q_L = \sum P_i^0 X_i^1 / \sum P_i^0 X_i^0,$$

where P_i^t and X_i^t represent the price and quantity of good i in time t. Since prices are held fixed at their base time-period levels, the Laspeyres index indicates how much of the change in value of total quantity resulted from pure quantity changes. A Laspeyres price index can similarly be specified in which quantities, used as weights, are held fixed at their base time-period levels.

The Paasche quantity index for inputs or outputs may be written:

$$Q_P = \sum P_i^1 X_i^1 / \sum P_i^1 X_i^0.$$

In contrast to the Laspeyres quantity index, prices (rather than quantities) are held fixed at their new levels. The Paasche price index holds quantities, used as weights, fixed at their current levels.

In summary, the Laspeyres quantity index weights the individual quantities to be aggregated with base time-period prices; the Laspeyres price index weights with base time-period quantities; the Paasche quantity index weights with current prices; and the Paasche price index weights with current quantities.

The Laspeyres and Paasche indices provide approximations to intertemporal changes which capture only the two most extreme classes of changes in the composition of the aggregate: either perfect or no substitution among the individual elements of the aggregate. (This is because the indices correspond to linear or fixed-coefficient/Leontief aggregator functions.) If, over time, substitution among inputs or outputs occurs, the indices can provide biased measures of the true aggregate either because substitution is not allowed or perfect substitution occurs.

Tornqvist and Fisher Ideal indices—The Tornqvist and Fisher Ideal indices provide more accurate approximations to changes than the Laspeyres or Paasche indices because intermediate substitution possibilities are incorporated. The individual components (e.g., species) of the aggregate (e.g., total catch) do not have to be either perfect or nonsubstitutes; instead, intermediate substitution possibilities are allowed. This occurs because the prices or quantities from both time periods under comparison enter the index to account for the possible changes in the mix of the inputs or outputs of the index.

The Tornqvist quantity index may be specified:

$$Q_T = \Pi_i [X_i^1 / X_i^0] 0.5 (S_{i1} + S_{i0}),$$

where X_i^k is the value of the ith price or quantity in time k, S_i^k is the share of total revenue (cost) in time k of output (input) i, ln denotes natural logarithm, and Π_i is the product operator. Revenue or cost shares are used as weights.

The Fisher Ideal index is the geometric mean of the Laspeyres and Paasche indices, and may be written as:

$$Q_F = [\sum S_i^1 (X_i^1 / X_i^0) / \sum S_i^0 (X_i^1 / X_i^0)]^{0.5}.$$

In order to empirically assess the differences among the Laspeyres, Paasche, Tornqvist, and Fisher Ideal index formulae, this study computes all four types of output indices in each of the four regions and for all regions combined. Part 2 provides additional theoretical discussion on this general topic.

Chain and fixed-base indices

Indices may be formed by either the chain or fixed-base methods. The fixed-base procedure directly compares all changes in prices, quantities, or total-factor productivity to some initial base period. The base period may remain constant or may be changed after some period of time.

Fixed-base indices can be expressed in general form as:

$$P_{0t} = P_t / P_0,$$

where P_{0t} represents the fixed-base index comparing price in time t with that of base time 0, P_t is price in time t, P_0 is price in the initial time 0, and the prices are calculated by some index-number formula (e.g., Laspeyres or Tornqvist).

Chain indices directly compare adjacent observations in a sequence of index numbers. Nonadjacent observations are compared indirectly by using the intervening observations as intermediaries. This practice results in transitive comparisons. The general form of the chain index can be written:

$$P_{0t}^{ch} = P_{01} \times P_{12} \times P_{23} \times \ldots \times P_{t-1},$$

where each individual term, P_{ij}, is computed by the index-number formula used, and represents the change from time period i to time period j $[i < j]$. P_{0t}^{ch} thus compares output in time t with output in time 0, the base time period. This formula reflects the basic relationship:

$$P_t / P_0 = P_1 / P_0 \times P_2 / P_1 \times \ldots \times P_t / P_{t-1}.$$

Since all values are represented in terms of the reference period 0 (in this study, 1981), comparisons between adjacent time periods, say i and $i-1$, are achieved with the following formula:

$$P_i = P_{0i} / P_{0i-1}$$

where $0 < i-1 < i < t$.

The values used to weight the individual quantities or prices (aggregated into a composite quantity or price) are kept up-to-date in the chain index, while the fixed-base index compares time periods for which the weights can be very different. As producers change their production patterns in response to changes in relative price, fixed-base indices maintain weights which may have changed and are no longer representative of current output or input mixes. Chain indices are generally preferred on *a priori* grounds for these reasons.

This study empirically assesses the fixed-base and chain indices for total output in each region and the entire fleet. Additional methodological discussion is provided in Part 2 for interested readers.

Bilateral and multilateral indices

Two basic types of indices can be used, bilateral and multilateral. Bilateral indices provide intertemporal comparisons of total-factor productivity (TFP) for any region or interspatial comparisons between regions for any given time period. Because of the large number of possible binary combinations which are not necessarily transitive, bilateral indices are inappropriate for comparisons that are not binary (e.g., TFP in region *i* in time *t* with TFP of region *j* in time $t+1$).

The Tornqvist bilateral index of total-factor productivity can be written:

$$\begin{aligned} \ln TFP_k - \ln TFP_l = & \textstyle\sum_i 0.5\,(R_{ik} + R_{il})[\ln Y_{ik} - \ln Y_{il}] \\ & - \textstyle\sum_i 0.5\,(W_{ik} + W_{il})[\ln X_{ik} - \ln X_{il}], \end{aligned}$$

where *k* and *l* are adjacent time periods (or regions), the Y_{ij} are output indices for output *i* of time *j*, the X_{ij} are input indices for input *i* of time *j*, the R_{ij} are product revenue shares, and the W_{ij} are input cost shares.

Multilateral indices have been proposed by Caves et al. (1982a) to provide transitive comparisons in a multilateral setting. Transitive comparisons are achieved by making all possible binary comparisons in terms of the geometric mean of all observations. For example, any two regions in different time periods are compared with each other by comparing both with the geometric mean.

Multilateral indices directly compare adjacent and nonadjacent observations but only by destroying the fixity of historical comparisons. As additional observations are added over time, thereby expanding the set of comparisons, the multilateral index changes because the geometric mean of the observations changes. In contrast, bilateral indices do not directly compare nonadjacent observations and the historical comparisons remain intact.

The Tornqvist multilateral index for total-factor productivity (TFP) may be written (Caves et al. 1982a):

$$\begin{aligned} \ln TFP_k - \ln TFP_l = & \textstyle\sum_i 0.5\,(R_{ik} + R_i^*)[\ln Y_{ik} - \ln Y_i'] \\ & - \textstyle\sum_i 0.5\,(R_{il} + R_i^*)[\ln Y_{il} - \ln Y_i'] \\ & - \textstyle\sum_i 0.5\,(W_{ik} + W_i^*)[\ln X_{ik} - \ln X_i'] \\ & - \textstyle\sum_i 0.5\,(W_{il} + W_i^*)[\ln X_{il} - \ln X_i'], \end{aligned}$$

where an asterisk associated with a variable indicates the arithmetic mean, and an an apostrophe indicates the geometric mean.

This study empirically evaluates the bilateral and multilateral procedures for all of the indices computed. The Tornqvist formula is used because it is the only one for which the theoretical properties of both the bilateral and multilateral indices have been examined. Additional discussion is provided in Part 2.

Economic performance index

Norton et al. (1985) present an index of industry economic performance which attempts to measure economic performance over time or space. The index recognizes that economic performance could change due to changes in prices as well as productivity. The index incorporates the effects upon industry of economic performance of real prices for aggregate output, aggregate input, and total-factor productivity.

The economic performance index in general form may be written:

$$EP_{kl} = TFP\ (P_{kl}^{Y} \,/\, P_{kl}^{X}),$$

where *TFP* again refers to total-factor productivity, P^Y refers to an aggregate-output price index, P^X refers to an aggregate-input price index, and *k* and *l* refer to time periods or regions.

This study provides economic performance indices using the Tornqvist direct-chain index of TFP and the Tornqvist implicit real-price chain indices of agregate output and aggregate input. Both bilateral and multilateral indices are formed.

The economic performance index is developed through an *ad hoc* procedure and the theoretical properties of the index are unknown. For example, when productivity is increasing (decreasing) and the price ratio is widening (narrowing), the results are unambiguous: industry economic performance is improving (declining). However, when productivity is increasing (decreasing) and the price ratio is narrowing (widening), the overall effect is not clear. Instead, the systematic properties of the index require further analysis, and results should therefore be treated as preliminary.

Data and index construction

Introduction

This section provides a description of the sources and methods used in the construction of the panel (pooled cross section and time series) data set used for analysis of the Pacific trawl fleet.

Output indices

The output indices are developed for U.S. vessels with landings in Washington, Oregon, and northern and cental California which harvest in the fishery conservation zone for years beginning in 1981. The Washington landings exclude fish harvested in Puget Sound but do include vessels harvesting in the fishery conservation zone and landing in Puget Sound ports. The northern California or Eureka region includes landings in ports in the Crescent City, Eureka, and Fort Bragg areas. The central California or Monterey region includes landings in ports in the Bodega Bay, San Francisco, and Monterey areas. Nine species assemblages are specified: Dover sole, Petrale sole, other flatfish, rockfish, Pacific cod and ling cod, sablefish, pink shrimp, and Pacific whiting.

The output indices require total dollar value and total pounds of landings for each geographical region and each year for each species of concern. The revenue and catch data are from the PacFIN Management Database. All species and market categories within each of the nine species groups are linearly aggregated. The Pacific whiting species category includes fish harvested by both domestic and joint-venture vessels. Joint-venture whiting revenue and landings data are apportioned between Washington and Oregon in the Columbia area according to the home ports of the joint-venture whiting vessels. Revenue shares by region are reported in Table 17.

Input indices

Three major categories of inputs are distinguished: labor, capital, and fuel. The share or proportion of each input in total costs by region is reported in Table 33.

Labor index—The labor input indices are constructed from three categories of labor: ordinary crewmember, engineer, and captain. Total crew size is currently unavailable for the fleet, but since most vessels have a total crew of three (captain, engineer, and ordinary seaman), all vessels are assigned this crew size. Greater refinement will be possible as more information becomes available. As such, the labor indices presented in this study are strictly preliminary and may be subject to revision after refinement of the database.

Crew sizes are stock values and alone do not provide a satisfactory measure of the annual flow of labor services. Crew sizes are converted into annual flows of labor services by multiplying the number of people in each labor category in each region and time period by the corresponding measure of fishing time used in the study, the number of landings (discussed below). The flow of labor services is thus in man-landings per year.

Quality adjustments of effective annual flows of labor services are not possible with the level and extent of data available. For example, Jorgenson and Griliches (1967) adjust for changes in the quality of labor due to changes in the educational composition of the labor force. In fishing industries, years of fishing experience would be desirable. Ideally, the flow of labor services could also be adjusted for changes in labor efficiency that accompany changes in intensity of effort or time per person (Denison 1962).

Each labor category is valued at its opportunity cost.[1] This provides an exogenous representation of both remuneration to labor and food costs. The data sources include:

(1) *County Business Patterns* for California, Oregon, and Washington, Bureau of the Census, U.S. Department of Commerce, Wash., D.C.

(2) *Area Wage Survey of Grays Harbor and Pacific Counties 1984*, Labor Market and Economic Analysis Branch, Washington State Employment Security Department, Olympia, WA 98504.

(3) *Oregon Occupations, 1984-85*, Oregon Career Information System, University of Oregon, Eugene, OR 97403.

(4) *Area Wage Survey*, Bureau of Labor Statisitics, U.S. Department of Labor, Wash., D.C.

(5) *Area Planning Information*, Employment Development Department, State of California, Sacramento, CA 95814.

All mean annual incomes used for opportunity costs in all labor categories are in 1981 dollars after deflation by the GNP implicit price index.

The opportunity cost of crew labor is an economic measure based upon reported earnings of workers in the counties in which the trawlers are homeported. Data on mean annual income for ordinary crewmembers are from source (1) above, where the opportunity cost is assumed to be the mean wage earned in manufacturing, transportation, and retail trade sectors. Captains are assumed to have managerial and entrepreneurial skills which imply a higher opportunity cost than for ordinary crewmembers. For lack of any specific alternatives, captains are given an opportunity cost 20 percent higher than ordinary crewmembers. The same data source is used as for ordinary crewmembers.

Vessel engineers are assumed to have an annual opportunity cost equivalent to the wages of an auto mechanic in their home ports (complete data are not available for the preferred category of diesel mechanic). Hourly wage rates for individual California ports are obtained from source (5). Since these wage rates for experienced journeymen auto mechanics are given only in ranges, the midpoint of each year's range is selected. Because data prior to 1984 are usually absent, these rates are assumed to change year-to-year at the same proportional rate of change as in San Francisco, where more timely data are obtained from source (4). Hourly wage rates for Oregon coastal auto mechanics are obtained for 1984-85 from source (3), and are assumed to change over time at the same rate as Portland auto mechanics, from source (4). Hourly coastal Washington auto mechanic rates are obtained for 1984 from source (2), and are assumed to change at the same rate as Seattle wages, from source (4) for previous years. Auto mechanics are assumed to work 40 hours per week, 50 weeks per year.

The home port of each vessel in every year is not known because home ports are obtained from the PacFIN Research Database, whose timeliness lags the annual vessel inventory used to compile annual numbers of vessels by region. Moss Landing is selected as the representative port for central California, Crescent City for northern California, Newport for Oregon, and Westport (Grays Harbor) for Washington.

In order to compute a single index of real labor input services for each region, a Tornqvist multilateral index is employed:

$$\begin{aligned}\ln L_k - \ln L_l = {}_1\Sigma_3\, 0.5\,(W_{ik} + W_i^*)[\ln L_{ik} - \ln L_i'] \\ - {}_1\Sigma_3\, 0.5\,(W_{il} + W_i^*)[\ln L_{il} - \ln L_i'].\end{aligned}$$

where L_{ik} is the quantity of labor services in the ith labor category for the kth (time-differentiated) region, L_k is the aggregate index of labor input for the kth region, W_{ik} is the compensation share for category i in region k, W_i^* is the arithmetic mean over all regions and time periods of compensation shares for category i, and L_i' is the geometric mean of the number of labor services in category i over all regions and time periods. A Tornqvist bilateral labor index is also constructed for use in the Tornqvist bilateral TFP and aggregate input indices. Tornqvist multilateral and bilateral chain aggregate labor indices are reported in Table 29 and Table 30, respectively.

Fuel index—Fuel consumption rates are estimated following an economic-engineering procedure. Annual fuel cost data for 120 vessel-years covering the 1981-83 period are divided by port-specific mean annual prices for cash purchases of No. 2 marine diesel fuel for 400-gallons. The estimate of annual fuel consumption for each vessel is then divided by its respective number of landings to give its mean fuel consumption per landing by region. Average fuel consumption per landing is then calculated for all vessels in each region. Each region's total annual fuel consumption is then derived by multiplying the regional mean fuel consumption per landing by the total number of landings in each year for that region. All vessels are assumed to use diesel fuel rather than gasoline. All prices are deflated by the GNP implicit price index to provide constant 1981 dollars. Fuel cost data are from confidential federal financial statements.

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[1] In economics, the term "opportunity cost" describes the cost of undertaking a particular activity in terms of the foregone benefits of the next-best alternative. Thus the opportunity cost to capital owners is usually specified to be the interest they could receive if they placed this money in a financial institution. Similarly, the opportunity cost to a fisherman is the wage foregone (or opportunity lost) to this person by not working in the next-most-rewarding alternative.

Annual diesel fuel cash prices are for 400 gallons of No. 2 marine diesel fuel. The 1981-83 port prices were obtained in the following manner. First, 1985 prices from marine fuel docks in each sample port were obtained by telephone interviews in February, May, and November with operators of marine fuel docks from 31 ports in Washington, Oregon, and California. These 1985 prices are averaged and deflated to 1981 levels by the GNP implicit price index, and are assumed to vary over time at the same rate as diesel fuel prices at petroleum terminals in San Francisco, Portland, or Seattle reported in *Platt's Oilgram Price Report: An International Daily Oil/Gas Price and Marketing Letter* (McGraw-Hill). It is reasonable to assume that individual port prices follow prices at major oil terminals, since marine-fuel dock port prices are essentially established on a formula basis from the terminal prices. Regional Tornqvist bilateral and multilateral chain indices for fuel are reported in Tables 29 and 30, respectively.

The total number of landings for Washington vessels of U.S. ownership fishing in the fishery conservation zone and landing anywhere in Washington is from the Washington Department of Fisheries, Olympia, WA 98504, while the number of landings for the other three regions is from the PacFIN Management Database. Joint-venture vessels' fishing time is calculated in weeks of fishing, where the beginning and ending dates of each vessel's fishing season are obtained from logbooks for the years 1981-84. The total number of days for each vessel is then divided by 7. When more complete information becomes available, the number of actual days fished can be taken from the logbooks rather than the beginning and ending dates of a season.

Capital index—The quantity of capital actually used in production is not the stock of capital (e.g., the number of vessels) but the flow of productive services from this capital stock. Thus more services for production are available from vessels actually fishing than from the same vessels tied up in ports.

The price of these capital services is a rental price for capital services on organized markets (e.g., tool rental). When capital services are not exchanged on markets, costs are imputed to firms to reflect the opportunity cost to capital owners of their money tied up in the capital stock and the depreciation of the capital equipment (Jorgenson 1974).

The capital services price per vessel for any given year (t) and size class (j) is given by:

$$P_{kjt} = r_t P_{Aj} + d_t P_{Aj},$$

where P_{Aj} is the mean vessel acquisition price per vessel in size class j, r_t is the opportunity cost of capital in time t, and d_t is the depreciation rate. Depreciation measures the present value of all future declines in productive capability.

This capital services price is an imputed price, and provides an accurate measure of the economic value of capital services to capital owners when the stock of capital is in full static equilibrium in any given time period. That is, the actual capital services are equal to the optimum flow of services, and firms are capable of making the required adjustments to their stock of capital in order to attain the optimum amount in each year. When, for example, the existing capital stock is inadequate relative to demand, firms face a relative shortage of capital and have incentives to invest. An additional unit of capital then has an economic valuation greater than that measured by the capital services price. Alternatively, when the stock of capital is greater than that required for full equilibrium in any year, firms have a relative surplus of capital stock and incentives to disinvest or even leave the industry. In this case, the economic valuation of capital services is lower than the measured imputed price. This study assumes that capital is in full static equilibrium and that the imputed price of capital services accurately measures the economic value of these services.[2] The value of all capital services is also assumed equal to the sum of the values of the individual capital services (Christensen and Jorgenson 1969, 1970). Aggregation from the firm to the industry is therefore assumed possible.

P_{Aj} is expressed in 1981 prices, and is the mean vessel acquisition price per vessel from vessels purchased 1976-82. Of the total 106 vessels used to calculate these vessel acquisition prices, 15 are class I (1-49 registered feet), 81 are class II (50-74 registered feet), and 10 are class III (75+ registered feet). The vessel acquisition prices are from confidential financial statements. Stable and consistent functioning of capital markets and industry expectations are assumed after the Magnuson Fishery Conservation and Management Act was announced, but no changes are assumed after this time. Limited data require the assumption of no capital gains or losses. The relatively limited number of years for vessel acquisition prices mitigates the effects of capital vintage. Property taxes are not applied to fishing vessels on the U.S. west coast, and are therefore not included in the capital services price.

The opportunity cost of capital in any year, r_t, is assumed equal to the annual corporate bond rate on seasoned issues rated BAA by Moody's, reported in the *Federal Reserve Bulletin* of San Francisco. The annual depreciation rate is set at 7 percent, as suggested by the Southwest Regional Office of the National Marine Fisheries Service, NOAA, Terminal Island, California, and roughly (but not exactly) corresponds to straight-line depreciation with a 15-year economic life and zero scrap value of the vessel and gear.

The price of capital services is used in constructing the index of capital services for the fishery. Constructing this index requires weights that reflect the annual capital cost. The annual capital cost of vessels in each region and year for each length class is estimated as the product of the number of vessels and the annual price of capital services per vessel. The capital services price is assumed constant across regions due to the general mobility of vessels.

The index of capital services also requires annual quantity flows of capital services. The first step in measuring the flow of capital services is to collect annual vessel counts. These are compiled by the National Marine Fisheries Service at Terminal Island, California (Korson 1981-85). Northern and central California vessels since 1985 are assumed to have the same home ports on a percentage basis as those of the 1984 vessels in the PacFIN Research Database in La Jolla, CA. Three vessel size-classes based on Coast Guard registered length are distinguished: 1-49 ft; 50-74 ft; 75+ ft. The assignment of home states for a few vessels in the annual vessel inventories is inconsistent with the home port classification of the PacFIN research database, in which case the PACFIN assignment is followed.

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[2] Current research is in the process of incorporating variations in capacity utilization of capital following the procedure of Hulten (1986) and Berndt and Fuss (1986). This procedure adjusts the price of capital services rather than the stock of capital. The same research is accounting for changes in population abundance of the resource stock and variations in its catchability.

The annual vessel counts are stocks of capital potentially available for productive purposes in any given year. This study assumes that all vessels fully utilize the potential productive capacity available in each year, that is, the firms are at full static equilibrium in capital. Capital services are therefore assumed to be proportional to capital stocks. Ongoing research will relax this assumption.

The index of real capital services is aggregated over the three vessel length-classes by the Tornqvist multilateral index formula:

$$\begin{aligned}\ln K_k - \ln K_l = {}_1\Sigma_3\, 0.5\ (W_{ik} + W_i{*})[\ln K_{ik} - \ln K_i'] \\ - {}_1\Sigma_3\, 0.5\ (W_{il} + W_i{*})[\ln K_{il} - \ln K_i'].\end{aligned}$$

where K_{ik} is the number of vessels in size class i for the kth (time-differentiated) region, K_k is the aggregate index of annual capital services for the kth region, K_i' is the geometric mean of the number of vessels in category i (over all regions and time periods in i), W_{ik} is the kth region's share of total annual vessel capital cost attributed to vessels of type i, and $W_i{*}$ is the arithmetic mean of annual capital costs of vessels in class i (over all regions and time periods in i). Tornqvist bilateral indices are also constructed for use with the Tornqvist bilateral aggregate input and TFP index numbers. Tornqvist multilateral and bilateral capital chain indices are reported in Tables 29 and 30, respectively.

Empirical results

Introduction

This section has three objectives: (1) Review the empirical results and relate them to industry events; (2) evaluate empirically the different types of index procedures; and (3) assess the sources of available data.

The empirical results are reported in Tables 6 through 36. These tables include annual indices by region and fleet of total-factor productivity (TFP), TFP growth rates, aggregate output, each individual output, aggregate input, each individual input, implicit prices, and an index of industry economic performance in the spirit of Norton et al. (1985). Revenue and cost shares are also reported. Tornqvist multilateral and bilateral chain indices are reported for all categories in order to evaluate the multilateral and bilateral indexing approaches. Laspeyres, Paasche, Fisher Ideal, and Tornqvist fixed-base indices for aggregate outputs are reported in Tables 21-24 in order to empirically evaluate fixed-base versus chain indices and to evaluate the four different types of index formulae.

The growth-accounting results presented here assume constant returns to scale, full capacity utilization, technical efficiency, and marginal cost pricing. The empirical results are strictly preliminary and may be subject to revision because crew sizes and detailed vessel counts require additional refinement.

The Pacific trawl fleet

The bilateral total-factor productivity (TFP) indices are reported in Table 7. The empirical results indicate a substantial decline in productivity during 1982 and 1983 compared with 1981. Total-factor productivity then grew in 1984 and 1985. Fleet TFP grew at an average growth rate of nearly 0.38% for the industry over 1981-85 with particularly strong growth for 1984-85 (Table 9).

The 1982-83 multifactor productivity decline may largely be due to the harvesting of widow rockfish at levels beyond estimates of maximum sustainable yield and the decline of the pink shrimp fishery (Table 13). Rockfish and pink shrimp are the two most important species groups by share of total revenue (Table 16). Fleet aggregate output as a whole declined by 1.3% in 1982 and 0.47% in 1983 (Table 15). General increases in aggregate input also contributed to the 1982-83 decline in TFP (Table 26). Industry aggregate input usage grew by 8.73% in 1982 and 1.28% in 1983 (Table 28).

The TFP rise in 1984 and 1985 (Tables 7 and 9) can be attributed to an important decline in aggregate input usage from the 1983 level (Table 28). Industry aggregate output declined by 0.46% in 1984 and grew by 2.65% in 1985 (Table 15). No individual species appears to dominate the general rise in aggregate output, although pink shrimp landings were up (Table 13), and in 1985 pink shrimp constituted 29% and 22% of total revenue in Washington and Oregon, respectively (Table 16), and 16% of fleet revenues (Table 18). Fleet aggregate input declined by 11% in 1984 and by 1.5% in 1985 (Table 28).

Capital is an important component of aggregate input in terms of cost share (Table 33). Table 30 reports individual capital indices. Capital began to decline in Washington in 1983, while northern and central California experienced increases in capital in 1983 before a decline in 1984. Vessels may have transferred from Washington and Oregon to California in 1983. A number of vessels may also have left the active fleet due to sinkings, burnings, or financial difficulties. Other vessels, particularly larger ones, are known to have transferred fishing activities to Alaska.

Additional factors may have contributed to the 1984-85 rise in TFP. It is likely that the vessels leaving the fishery were relatively inefficient harvesters, in which case TFP would increase if many of the remaining vessels were operated by skippers and crews with fishing skills superior to those vessels that left the active fleet. The larger vessels that transferred to Alaska may have been more inefficient than medium and smaller vessels under the reduced level of resource abundance. This could be due to decreasing overall returns to scale as stocks, particularly widow rockfish, declined. As those larger vessels left the fleet, productivity measures of the remaining vessels should have increased. Productivity may also have increased as fishermen became more skilled with the technological innovations previously introduced in the production process (an increase in technical efficiency).

Regional differentials in total-factor productivity growth are demonstrated by the bilateral total-factor productivity indices reported in Table 7. By 1985, total-factor productivity for the entire fleet, and in Washington and Oregon surpassed 1981 levels, but not in northern and central California. Tables 14 and 26 indicate that the 1985 aggregate output level is below the 1981 level in Oregon and northern California regions and for the fleet, but that important regional variations exist in input usage. While input usage in Washington and Oregon remains well below 1981 levels, and in fact continued to decline through 1985, input usage in California is still above the 1981 level.

Fleet economic performance depends upon the real prices of outputs and inputs in addition to total-factor productivity. Tornqvist bilateral implicit chain indices for constant-dollar aggregate output prices and aggregate input prices are reported in Tables 20 and 32, respectively.[3] By 1985, aggregate output real prices increased above 1981 levels for the entire fleet and northern and central California while remaining below 1981 levels for Washington and Oregon. By 1985, aggregate input real prices for the fleet had remained below 1981 levels, while the 1985 aggregate input prices rose above the 1981 level for Washington. The general increase in aggregate output price and a general decline in aggregate input price by 1985 suggest an improvement in the ratio of product price to input price for the Pacific trawl fleet which reinforced the recent gains in TFP. On the whole, the economic performance of the fleet should have returned to 1981 levels although economic conditions for individual vessels may differ.

Economic performance

The economic performance index of Norton et al. (1985) attempts to combine indices of prices and productivity into a single measure of fleet economic performance. Tornqvist bilateral chain economic performance indices are reported in Table 36. As discussed above, the results should be interpreted with caution due to the uncertain theoretical basis of these indices.

The indices indicate that overall fleet economic performance in 1985 is above that of the initial time period, 1981. Reinforcing recent productivity gains are the general increase in aggregate output price and general decline in aggregate input price as noted above.

Methodological evaluation

Multilateral vs. bilateral indices—Comparisons of mutlilateral and bilateral indices are made for the Tornqvist chain indices. These indices are computed for total factor productivity (TFP) in Tables 6 and 7, aggregate outputs in Tables 11 and 14, individual outputs in Tables 10 and 13, aggregate inputs in Tables 25 and 26, and individual inputs in Tables 29 and 30.

All of the multilateral indices are normalized in terms of 1981 Washington by dividing all values by the value of 1981 Washington. Setting 1981 Washington equal to 1.00 provides a more convenient basis for making comparisons. All relative relationships are preserved by normalization. Multilateral indices for the fleet are similarly normalized in terms of the 1981 value.

The computed Tornqvist multilateral and bilateral chain indices generally differ little from one another in tracking turning points (i.e., increase to decrease or decrease to increase) and trends. For example, both sets of TFP indices (Tables 6 and 7) indicate productivity declines in 1982 or 1983 and agree with the occurrences of all increases and decreases. This coincidence of turning points occurs because the growth rates of multilateral and bilateral indices generally differ little in magnitude.

Similarity in growth rates can be demonstrated for the most important index, the total-factor productivity index, by regressing the 1982-85 multilateral growth rates upon the 1982-85 bilateral growth rates with an intercept term. Using this result, it is possible to (1) test to determine whether the intercept term is significantly different from zero and thus whether one set of growth rates over- or understates growth by a fixed percentage relative to the other; (2) test to determine whether the slope coefficient is significantly different from unity as a check on the proportionality of one set of growth rates to another; and (3) examine the R^2 as a measure of the linear proximity of the two sets of growth rates. Regressing the multilateral TFP growth rates upon the bilateral TFP growth rates produces the expected result: the intercept is not significantly different than zero, the slope is not significantly different from unity, and the R^2 is very high. (Intercept coefficient = 0.005, S.E. 0.005; slope coefficient = 1.054, S.E. 0.031; R^2 = 0.984, and F-statistic for overall regression = 1123.004.)

Comparability between the multilateral and bilateral indices is diminished at the highest levels of aggregation, because relatively minor differences for individual outputs and/or inputs begin to accumulate at higher levels of aggregation. For example, proportionately greater differences are exhibited among TFP indices than among individual outputs or inputs. Thus the regional individual species indices (Tables 10 and 13) track individual outputs by region in a similar manner, but the 1983-84 indices for the fleet (Tables 11 and 14) differ (the multilateral index indicates a small increase, whereas the bilateral index indicates a slight decrease).

Although the multilateral and bilateral indices nearly always agree on turning points and usually agree on trends and growth rates, the magnitudes of the indices relative to the initial year (1981) can nonetheless differ in important ways.

To formally compare the magnitudes of multilateral and bilateral TFP indices (rather than growth rates), the multilateral TFP index is regressed upon the bilateral TFP index for the years 1982-85 with an intercept term. The estimated intercept coefficient is 0.319 (S.E. 0.250), the estimated slope coefficient is 0.577 (S.E. 0.266), the R^2 is 0.208, and the overall F is 4.707. These results suggest that a fixed displacement between indices does not exist but that the multilateral TFP measures tend to be about 40 percent lower than the bilateral TFP measures. The R^2 of 0.21 suggests that an additional 79 percent of the variation in the multilateral index estimates exists after the 40 percent proportionality difference has been accounted for (Hazilla and Kopp 1984a,b).

The principal reason for the difference in magnitude relative to the initial year lies in interpretation of the index. The multilateral index for the initial year represents deviations from the geometric mean (of all regions and years), while the bilateral index for the initial year is the constant value 1. That is, the multilateral and bilateral initial values can differ considerably because of the different initial-period magnitudes. This difference is accentuated if the initial year differs markedly from the geometric mean of all years and regions. Both base year and chain multilateral indices are affected by the difference in interpretation of the initial time period.

The computed multilateral and bilateral indices also differ markedly in the years 1982-85 when an intertemporal change occurs which is substantially different from the geometric mean and the value of the preceding year. Consider the Pacific whiting multilateral and bilateral output indices. The Pacific whiting catch from joint-venture vessels is relatively large in total tonnage and can vary considerably from year-to-year and region-to-region.

The computed multilateral and bilateral indices can also differ in an important way when very small intertemporal changes occur. The bilateral index can track the small change but the multilateral index can fail to pick up a change in trend from increasing to decreasing or vice versa, because all of its comparisons are in terms of the geometric mean. Thus the multilateral procedure tracks turning-points most effectively when the values are closer to the geometric mean, but may experience difficulties when all the values are substantially different from the geometric mean.

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[3] Implicit prices are calculated through Fisher's weak-factor reversal test. This relationship states that the product of the price index and the quantity index should equal the expenditure ratio between the two time periods. Part 2 and Appendix 3 provide additional discussion.

In summary, the multilateral index has superior theoretical properties to the bilateral index, but can demonstrate empirical limitations in relatively extreme situations. Fundamentally comparable results are demonstrated with the two indices. However, for official reports likely to receive widespread distribution, the bilateral procedure should be used since fixity of historical comparisons remains intact (explanations are not required when different numbers occur in subsequent years) and interpretations are easier.

Chain vs. fixed-base indices—As noted above, fixed-base indices compare all changes to some initial base period, while chain indices make comparisons by a process of chaining binary (period-to-period) comparisons back to the original time period (in this case, 1981).

Table 14 reports Tornqvist bilateral chain indices of total output by region, and Table 24 reports Tornqvist bilateral fixed-base indices of total output by region. Comparison between the two tables indicates that very different results and types of information are provided by the two approaches. For example, the fixed-base indices indicate that 1985 total output is less than 1981 in all regions, while the chain indices indicate that 1985 total output is greater for Washington and central California. This difference may be due to the changing species composition of catch over time (see Tables 16 and 18) with which the fixed-base index procedure has difficulty in dealing. Although the choice between the two procedures is somewhat dependent upon the type of information to be presented, the chain procedure is generally preferred on theoretical grounds.

Laspeyres, Paasche, Fisher Ideal, and Tornqvist indices—As discussed above, a number of different index-number procedures exist, each index corresponding to different functional forms of the aggregator function and consequently each index number having different theoretical properties. The Laspeyres and Paasche indices implicitly assume either no or perfect substitution between individual commodities, while the class of superlative indices does not require commodities to be perfect or zero substitutes. Changes in the composition of an aggregate are therefore correctly captured.

To facilitate an empirical evaluation of these indices, fixed-base aggregate-output bilateral indices are developed for each region. Laspeyres indices are presented in Table 21, Paasche indices in Table 22, Fisher Ideal indices in Table 23, and Tornqvist indices in Table 24. An examination of Tables 21-24 indicates that different results are possible, depending upon the choice of index number. Consider, for example, the years 1983-85 for northern California: The Laspeyres and Fisher Ideal indices report a decline in landings from 1983 to 1984, with an increase from 1984 to 1985. In contrast, the Paasche and Tornqvist indices report continual increases.

The Fisher Ideal index lies between the values of the Paasche and Laspeyres indices as expected, since the Fisher Ideal index is the geometric mean of the Paasche and Laspeyres indices. Values of the Fisher Ideal and Tornqvist indices do differ.

As the degree of data disaggregation increases (so that a quantity may become zero), the Fisher Ideal index number formula remains well defined while the Tornqvist does not (because of the log transformation which is undefined when the untransformed variable is zero). The consequence of this property is clearly demonstrated in Tables 10 and 13 for Pacific whiting landings in Washington. In 1981, no landings of Pacific whiting were made in Washington by either the coastal fleet or joint-venture vessels. However, large landings in 1984 were reported by joint-venture vessels homeported in Washington (with landings consequently assigned to Washington). To allow a Tornqvist index number to be calculated for 1984, a small value is given to 1981 (an *ad hoc* procedure), but an enormous value is calculated for the Tornqvist index. This result carries over to the 1984 fleet value, where the Fisher Ideal (Table 23) indicates a decrease from 1983 to 1984 and an increase from 1984 to 1985. In contrast, the Tornqvist (Table 24) reports just the opposite result.

Recommended index-number procedure—The recommended index-number procedure for analysis with a widespread and disparate audience is either the Tornqvist or Fisher Ideal bilateral chain index. The major advantage of the Fisher Ideal is that it is well defined when the data are so highly disaggregated that a zero output or input occurs, while the Tornqvist is not. Chain indices are preferred to fixed-base indices. Multilateral indices have greater versatility than bilateral indices, but do not have fixity of historical comparisons. The Tornqvist multilateral chain index can be quite suitable for technically sophisticated audiences.

Data evaluation

The data currently available are sufficient for potentially satisfactory construction of productivity, quantity, and price indices for outputs and inputs. Nevertheless, certain limitations exist, many of which can be corrected or at least mitigated with time.

The PacFIN Management Database provides timely data for revenues and quantities of outputs. Fuel prices and interest rates are readily obtainable on a consistent and timely basis through telephone surveys and various issues of the *Federal Reserve Bulletin*, respectively. Wage and income data used to construct the opportunity cost of labor are available, but there is a 1-2 year lag in the most recent data of the Bureau of the Census. Nevertheless, this data lag does not do great harm to the analysis. Crew-size information for all vessels is currently incomplete, and scope for updating and refinement certainly exists.

Cost data from the NMFS confidential financial-cost database are adequate for the task at hand. The cost sample is not comprehensive for all vessels, nor is it systematically derived on the basis of sampling theory. Yet the rather large sample does provide a reasonable degree of confidence in its adequacy. This confidence should improve as the cost data are updated on a continual basis.

The Pacific whiting joint-venture data are among the least satisfactory of all the data currently available. The fishing-time information needs to be updated from logbooks and from confidential sources.

Refinement of the concept of a fisherman's opportunity-cost and better information about the most likely alternatives would improve the analysis. If the information was available, capital gains or losses, i.e., the revaluation of assets, could be important in computing the real cost of capital services (even though most capital gains are not realized). Little is known about the actual rate of economic depreciation of capital assets.

The use of an engineering approach to measuring fuel consumption may also be subject to limitations since the effects of changing economic conditions might not be fully incorporated into this procedure. Fuel consumption and more accurate fishing-time data may become available from logbooks. The quality of the analysis might improve in this case, and the engineering approach to measuring fuel consumption can be replaced by direct measurement. Finally, the absence of prices and the spotty and incomplete data on materials, supplies, ice, and other trip costs preclude their use in the analysis. In turn, this may lead to some form of omitted variable bias.

In summary, sufficient data of acceptable quality are available to construct output, input, and productivity indices. These data require additional refinement, upgrading, and updating to improve the quality of the analysis, particularly for crew sizes and vessel homeports. As such, the empirical results presented in this study are strictly preliminary, and may be subject to revision after final refinement of the database is completed.

Concluding remarks

This study is developed to address five issues of productivity measurement in the Pacific trawl fleet: (1) Apply the most recent advances in productivity measurement and the economic theory of index numbers; (2) utilize more extensive data sources than those previously used in productivity and performance studies of marine fishing industries; (3) evaluate the many different index-number procedures that are currently available; (4) clarify the meaning of productivity in marine fishing industries; and (5) collect into one accessible place the recent advances in productivity measurement and the economic theory of index numbers. Part 2 and its Appendices address task (5).

In conclusion, this study recommends the use of chain indices rather than fixed-base indices, either the Fisher Ideal or Tornqvist index, and bilateral indices for recurring publications. The data currently available are adequate for satisfactory construction of productivity, quantity, and price indices. Certain limitations do exist but are potentially correctable if existing efforts at the Southwest Fisheries Center (National Marine Fisheries Service, La Jolla, CA) aimed at expanding and updating economic bases are continued along their current lines. These current efforts include expanding and developing the PacFIN Research Database, logbook data, the cost database, and input prices.

PART 2

Additional topics in productivity measurement

This section considers several additional aspects of productivity measurement to supplement the general framework developed in Part 1. This section proceeds by first considering measurement of productivity by the growth-accounting framework using economic index numbers and by the structural framework using econometric methods. Next, the assumptions behind the growth-accounting framework are reviewed, followed by a discussion of interspatial and intertemporal productivity, and a review of duality-based measures of productivity.

Growth-accounting and structural frameworks

Total-factor productivity can be interpreted and measured by either the growth-accounting framework with economic index numbers or by the structural framework using econometric methods. The structural approach measures productivity change as the rate of technological progress when measured by a production, cost, revenue, or profit function. It also allows detailed examination of the structure of production, including measurement of economies of scale, tests for full static equilibrium (Kulatilaka 1985, Schankerman and Nadiri 1986), technical inefficiency (Nishimizu and Page 1982), and corrections for deviations from competitive markets and marginal cost pricing (Denny et al. 1981). This detailed information requires estimation of an econometric model.

The structural approach is parametric and global, since it can yield information about the full range of the estimated aggregate production or cost function and requires parametric specification of this function. The growth-accounting framework is nonparametric since it is based on Divisia indices of multifactor input and multifactor productivity. It is also local, since the only information about the nature of the production technology is embodied in the marginal productivity conditions. These conditions allow calculation of the slope of the aggregate production function using only relative prices, but only along the observed surface of the aggregate production function. The results are thus local to this observed range (Hulten 1986).

Assumptions of the growth-accounting framework

The growth-accounting framework for measuring total-factor productivity makes several assumptions: Constant returns to scale, technical efficiency, perfect competition in input and output markets, and full static equilibrium of all inputs. When these assumptions are not satisfied, conventional indices of total-factor productivity growth include not only the effect of technical change, but may also include some or all of the effects from nonconstant returns to scale, technical inefficiency, market imperfections, and departures from full static equilibrium.

Consider first the assumption of perfect competition: This assumption is in part acceptable in marine fishing industries. Most importantly, fishermen are generally pricetakers in the product and factor markets, but entry and exit may be difficult. Readers interested in the concept are referred to Kendrick (1973) and Denny et al. (1981). Consider next the returns to scale: Parametric representation of the production technology is necessary to identify and estimate the separate effects due to scale economies and technical change (Diamond et al. 1978, Chan and Mountain 1983). Once a measure of nonconstant returns to scale is available, the TFP index can be adjusted by dividing by the measure of scale economies (Caves et al. 1982b). Alternatively, James Kirkley (Va. Inst. Mar. Sci., Gloucester Point, VA 23062, pers. commun. Feb. 1987) suggests that the nonparametric method of Diewert and Parkan (1985) can be used to examine the effects of scale economies and technical change (although only the lower bounds can be examined).

Nishimizu and Page (1982) note that a distinction should be drawn between technological change and changes in the efficiency with which known technology is applied to production. Given a level of technology, explicit resource allocation may be required to reach the "best-practice" level of technical efficiency over time. After the adoption of a new technology (e.g., stern trawling), productivity gains are possible as firms master the new technology over time. A parametric approach is required to address this issue. The growth-accounting framework adopted in this study implicitly assumes that all firms are technically efficient, that is, that production is on the frontier of the industry-production function.

Fourth, consider the effects of vessels not in full static equilibrium in all of their inputs: If producers are assumed to be in long-run equilibrium when in fact they may be in short-run temporary equilibrium, the productivity residual may be systematically underestimated. (Berndt and Fuss 1986, Hulten 1986, Winston 1974). The traditional method for TFP measurement is appropriate only if the firm's output is always produced at the long-run equilibrium point, i.e., the point of tangency between the short-run unit or average total cost curve and the long-run unit cost curve. Instead, if there are divergences from static equilibrium, the firm is not operating along the long-run average cost curve, and the conventional measure of TFP includes variations in capacity utilization of the fixed inputs. For example, if a decline in overall resource availability or a change in its composition (species mix) causes a temporary equilibrium due entirely to underutilization of harvesting capacity, then a perfectly competitive fishing firm would not be in long-run equilibrium and measurement of TFP might be biased.

The problem of disequilibrium is corrected by one of two methods. Most frequently, the quantity of the quasi-fixed factor is adjusted to reflect the degree of capacity utilization (Jorgenson and Griliches 1967). Alternatively, the price of the fixed factor is adjusted to reflect its true shadow value, that is, the contributions of quasi-fixed inputs are valued at their shadow prices rather than market prices (Berndt and Fuss 1986). Morrison (1985a,b, 1986) provides further discussion on economic measures of capacity utilization obtained by econometric means, while Hulten (1986) and Berndt and Fuss (1986) discuss this in a growth-accounting framework. Current empirical research is addressing this issue.

Intertemporal and interspatial productivity

Intertemporal total-factor productivity can be interpreted as a rate of shift over time in a production function[4]. As discussed in Part 1, the mechanism generating these rates of change is usually assumed to be technological progress, so that measurement of technological change is equivalent to the measurement of a change in intertemporal TFP. The input effect is associated with movements along the aggregate-production function, while the multifactor productivity residual is associated with shifts in the aggregate production function. This interpretation is generally attributed to Solow (1957), Jorgenson and Griliches (1967), and Hulten (1975). Denison (1962) and Star (1974) instead stress a diversity of factors which might be captured in the residual total-factor productivity measure. Changes in total-factor productivity in marine fishing industries might also be due, in part, to changes in resource availability and species composition, since higher levels of resource abundance should allow any given input-bundle to harvest more outputs. Changes in resource availability might also impact upon capacity utilization of a quasi-fixed factor such as capital and upon the rate of fuel utilization.

Interspatial total-factor productivity has a somewhat different interpretation than intertemporal total-factor productivity. Interspatial total-factor productivity can be defined as the proportional differences in an index of outputs between different production regions (or firms) relative to the proportional differences in an index of inputs. Interspatial productivity differences arise not from the dynamic process of technological change, but rather from static differences in technology across producing regions (or firms). Interspatial productivity differences in marine fishing industries are also likely to directly reflect differences in resource availability and composition (and indirectly through economies of scale).

Duality-based measures of productivity

The growth-accounting model developed in Part 1 measures multifactor productivity as the residual output not accounted for by the share-weighted growth rates of the factor inputs. As Ohta (1975) notes, total-factor productivity can also be equivalently measured by the residual diminution in average cost not accounted for by the input prices (and changes in scale economies if constant returns to scale are not assumed). Although this result is not of importance in this study, its general outlines are developed along the lines of Hulten's (1986) discussion for the sake of completeness and because so much of the recent productivity literature is developed in terms of costs.

Under certain regularity conditions (McFadden 1978, Lau 1978), the existence of a cost function dual to the production function $\dot{Y} = f(K,L)$ is implied:

$$C(t) = C[P^K(t),\ P^L(t),\ Y(t),t] \qquad (1)$$

$$= P^K(t)K(t) + P^L(t)L(t),$$

where $K(t)$ and $L(t)$ are the cost-minimizing quantities of capital and labor, respectively. Under constant returns to scale, this can be written:

$$C(t) = B(t)c[P^K(t),\ P^L(t)]Y(t), \qquad (2)$$

where $c(t)$ is termed the unit cost function, since $C(t)/Y(t)$ is the average cost of producing $Y(t)$ under cost minimization.

The sources of growth implications of equation (1) are derived from Shephard's Lemma, which implies that $\partial C(t)/\partial P^K(t) = K(t)$ and $\partial C(t)/\partial P^L(t) = L(t)$. This implies that:

$$C(*)/C - Y(*)/Y = B(*)/B + S_K(P^K(*)/P^K) \qquad (3)$$

$$+ S_L(P^L(*)/P^L).$$

---

[4] Either full or partial equilibrium econometric models of production can be used.

This expression states that the growth rate of average cost equals the growth rate of the shift parameter, $B(*)/B$, plus a Divisia index of input prices. Under constant returns to scale, $PY = P^K K + P^L L = C$, implying that $A(*)/A = - B(*)/B$. In other words, real average cost decreases at a rate equal to the growth rate of the Hicksian efficiency parameter.

This result means that the total-factor productivity residual can be measured as the residual growth rate of output not explained by the Divisia index of inputs, or as the residual diminution rate of average cost not explained by the Divisia index of input prices.

Economic theory of index numbers[5]

Introduction

The economic theory of index numbers is concerned with the relationships between the properties of index numbers and the properties of the underlying aggregator functions they represent. The demonstration in recent years that numerous index-number formulae can be explicitly derived from particular aggregator functions implies that rather than starting the selection process with a number of index-number formulae, an aggregator function with desirable economic properties can be specified and the corresponding index-number procedure derived.

To be more concrete, consider price and quantity data for N commodities for two periods (or economic entities), $P^0 = (P_1^0, P_2^0, \ldots, P_N^0)$, $P^1 = (P_1^1, P_2^0, \ldots, P_N^1)$, $X^0 = (X_1^0, X_2^0, \ldots, X_N^0)$, and $X^1 = (X_1^1, X_2^1, \ldots X_N^1)$. A price index $PI(P^0,P^1,X^0,X^1)$ is defined to be a function of prices and quantities, while a quantity index $QI(P^0,P^1,X^0,X^1)$ is defined to be another function of observable prices and quantities for the two periods.

Aggregator functions

An aggregator function f is a particular formula or procedure for aggregating the price and/or quantity data into some price or quantity index. Thus an aggregator function for the quantity index QI would specify some particular functional form for $QI(P^0,P^1,X^0,X^1)$. The aggregator function for an input-quantity index is essentially a production function, while the aggregator function for an input-price index is a unit-cost function. The aggregator function for outputs is a unit-revenue function for prices and a factor-requirements function for quantities (Diewert 1974).

An index number, such as a quantity index, is exact for a particular functional form F of the aggregator function if the ratios of the outputs (the values of F) between any two periods or regions are identically equal to the index of outputs: $QI(P^0,P^1,X^0,X^1) = F(X^1)/F(X^0)$ (Diewert 1976).

Diewert (1976a) provides a strong argument for considering only flexible aggregator functions, that is, those aggregator functions which can provide a second-order approximation to an arbitrary aggregator function. Diewert (1976a) terms that class of index numbers that are exactly represented by flexible aggregator functions as superlative.

Fisher's weak factor-reversal test

PI and QI are generally assumed to satisfy Fisher's (1922) weak factor reversal test:

$$PI(P^0,P^1,X^0,X^1)QI(P^0,P^1,X^0,X^1) \tag{4}$$
$$= {}_i\sum\nolimits_N P_i^1 X_i^1 \; / \; {}_i\sum\nolimits_N P_i^0 X_i^0.$$

Fisher's weak factor-reversal test (4) states that the product of the price index multiplied by the quantity index should equal the expenditure ratio between the two periods. PI is to be interpreted as the ratio of the price level in period 1 to the price level in period 0, while QI is the ratio of the quantity levels of the two time-periods (or economic entities). Given either a price index or quantity index, the other function can be defined implicitly by Fisher's weak factor-reversal test (4).

Laspeyres and Paasche (mean-of-order-*r*) indices

The Laspeyres and Paasche indices have traditionally been the most widely used of all index numbers. They belong to the general class of mean-of-order-r indices.

Define the mean-of-order-r quantity index using period-1 shares as (Allen and Diewert 1981):

$$Z(P^0,P^1,X^0X^1) = ({}_i\sum\nolimits_N S_i^1 (Z_i^1/Z_i^0)1/i \qquad \text{for } r \neq 0 \tag{5}$$
$$= ({}_i II_N (Z_i^1/Z_i^0))S_{i1} \qquad \text{for } r = 0$$

where $S_i^1 = P_i^1 X_i^1 / i\sum N^{P_i} {}^1 X_i^1$.

Some well-known indices are special cases of the mean-of-order-r index. The Laspeyres quantity index may be written:

$$Q_L = \sum P_i^0 X_i^1 / \sum P_i^0 X_i^0 \tag{6}$$
$$= \sum S_i^0 (X_i^1/X_i^0),$$

where $S_i^0 = P_i^0 X_i^0 / \sum P_i^0 X_i^0$. Since prices are held fixed at their base period (or economic entity) levels, the Laspeyres index indicates how much of the change in value of total quantity resulted from pure quantity changes. Similarly, the Laspeyres price index may be written:

$$P_L = \sum P_i^1 X_i^0 / \sum P_i^0 X_i^0 \tag{7}$$
$$= \sum S_i^0 (P_i^1/X_i^0).$$

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[5] Frisch (1936) distinguishes three approaches to index number theory: (1) "statistical" approaches, (2) the test approach, and (3), the functional approach, now called the economic theory of index numbers by Samuelson and Swamy (1974). The statistical approach assumes that all prices are affected proportionately (except for random errors) by the expansion of the money supply. Therefore it does not matter which price index is used to measure the common factor of proportionality, as long as the index number contains a sufficient number of statistically independent price ratios. Theil (1960) provides a "neostatistical" approach. The test or axiomatic approach initiated by Fisher (1911, 1922) assumes that the price and quantity indices are functions of the price and quantity vectors pertaining to two periods. Tests are *a priori* reasonable properties that the price and quantity vectors should possess. However, not all *a priori* reasonable properties are consistent with each other, that is, there are various impossibility theorems. Moreover, the family of index-number formulae resulting from a consistent restricted set of tests is often not uniquely determined (Diewert and Parkan 1985).

The economic and test approaches to index-number theory can be partially resolved. After assuming explicit functional forms for the underlying aggregator function and cost-minimizing behavior by the producer, certain functional forms for the aggregator function can be associated with certain functional forms for index-number formulae. Many of the index-number formulae, such as Fisher's Ideal formula, have been suggested as desirable in the literature on the test approach to index-number theory (Diewert 1981).

The Paasche quantity index is also a specific form of the mean-of-order-r index, and may be written as:

$$Q_P = \sum P_i^1 X_i^1 / \sum P_i^1 X_i^0. \tag{8}$$

In contrast to the Laspeyres quantity index, prices are held fixed at their new levels. The Paasche price index may be specified as:

$$P_P = \sum P_i^1 X_i^1 / \sum P_i^0 X_i^1 \tag{9}$$

The Laspeyres quantity index weights with base prices; the Laspeyres price index weights with base quantities; the Paasche quantity index weights with current prices; and the Paasche price index weights with current quantities.

The Laspeyres and Paasche indices are exact for a Leontief or fixed-coefficients aggregator function f:

$$f(X) = min_i[X_i | a_i : i = 1,2,\ldots,N], \tag{10}$$

where a_i is a fixed constant. The Laspeyres and Paasche indices are also exact for a linear aggregator function f:[6]

$$f(X) = \sum a_i X_i i. \tag{11}$$

The Laspeyres and Paasche indices are thus exactly equal to their corresponding true indices if there is either no substitution between commodities or if there is perfect substitution between commodities. The Laspeyres and Paasche indices always offer a first-order approximation to the true index. Therefore, if substitution between commodities lies exactly or close to either no or perfect substitution, the Laspeyres and Paasche indices provide acceptable performances. However, the larger the time period or the greater the difference between the base and comparison levels, the greater the likelihood that substantial price changes may occur (leading to an intermediate substitution case) and the greater the misrepresentation of these indices. Kirkley (Va. Inst. Mar. Sci., Gloucester Point, VA 23062, pers. commun. Feb. 1987) also notes that if the production function from which the Laspeyres and Paasche indices is derived is convex, then the Laspeyres index overstates and the Paasche index understates, while if the production function is concave, then the Laspeyres index understates and the Paasche index overstates.

Geometric indices

The class of geometric indices is also used with some regularity in empirical work. The geometric indices are defined by:

$$Z_G = {}_iII_N\, (Z_i^1/Z_i^0)^{S_i}, \tag{12}$$

where $S_i^0 = P_i^0 X_i^0 / {}_i\sum_N P_i^0 X_i^0$ and $S_i^1 = P_i^1 X_i^1 / {}_i\sum_N P_i^1 X_i^1$. These indices are exact for a Cobb-Douglas aggregator function defined by:

$$f(Z) = A_0\, {}_iII_N Z_i^{A_i}, \tag{13}$$

where ${}_i\sum_N A_i = 1$. The geometric mean index is one example of (12) with an aggregator function like (13). Frisch (1936) notes that since the geometric index satisfies the circular test, there is no difference between the chain and direct (fixed-base) indices (discussed further below).

The Vartia I (1974, 1976b) index provides another example of one in which the aggregator function is Cobb-Douglas.[7] The Vartia I price index $P_V(P^0,P^1,X^0,X^1)$ may be written:

$$\ln P_V(P^0,P^1,X^0,X^1) \tag{14}$$

$$= {}_i\sum_N [L(P_i^1 X_i^1, P_i^0 X_i^0) / L({}_i\sum_N P_i^1 X_i^1, {}_i\sum_N P_i^0 X_i^0)] \ln(P_i^1/P_i^0),$$

where the logarithmic mean function L introduced by Vartia (1974) and Sato (1976) is defined by $L(a,b) = (a - b)/(\ln a - \ln b)$ for $a \neq b$ and $L(a,a) = a$. Thus for equation (14), $L(P_i^1 X_i^1, P_i^0 X_i^0) = (P_i^1 X_i^1 - P_i^0 X_i^0)/[\ln(P_i^1 X_i^1) - \ln(P_i^0 X_i^0)]$ and $L(\sum P_i^1 X_i^1, \sum P_i^0 X_i^0) = (\sum P_i^1 X_i^1 - \sum P_i^0 X_i^0)/[\ln(P_i^1 X_i^1) - \ln(\sum P_i^0 X_i^0)]$.

The Vartia I quantity index $Q_V(P^0,P^1,X^0,X^1)$ is defined by:

$$\ln Q_V(P^0,P^1,X^0,X^1) \tag{15}$$

$$= {}_i\sum_N [L(P_i^1 X_i^1, P_i^0 X_i^0) / L({}_i\sum_N P_i^1 X_i^1, {}_i\sum_N P_i^0 X_i^0)] \ln(X_i^1/X_i^0)$$

$$= \ln P_V(X^0,X^1,P^0,P^1),$$

i.e., the price and quantity indices have the same functional form except that the roles of prices and quantities are interchanged. The Vartia I price and quantity indices satisfy the Fisher factor-reversal test (4) and have the property (defined below) of consistency in aggregation (Diewert 1978).

Diewert (1978) further notes that the Vartia I index approximates to the second order any superlative index. Thus the Vartia I (and geometric mean) index $Z_V(P^0,P^1,X^0,X^1)$ will be close to any superlative index $Z_S(P^0,P^1,X^0,X^1)$ provided that P^0 is close to P^1 and X^0 is close to X^1. Diewert calls this type of index pseudo-superlative. Moreover, this property holds without the assumption of optimizing behavior on the part of economic agents, since this property is founded upon theorems in numerical analysis rather than economics.

Diewert (1978) further suggests that the Vartia I price and quantity indices have serious defects which preclude their empirical applications. The Vartia I quantity index has the property such that rescaling the prices in either period will generally change the index, (i.e., in general $Q_V(TP^0,P^1,X^0,X^1) \neq TQ_V(P^0,P^1,X^0,X^1)$ for $T \neq 1$), while the Vartia I price index has the property such that rescaling the comparison period (or economic entity) price does not in general change the value of the price index by the same scale factor (i.e., in general, $P_V(P^0,TP^1,X^0,X^1) \neq TP_V(P^0,P^1,X^0,X^1)$ for $T \neq 1$).

Quadratic mean-of-order-*r* (superlative) indices

Quadratic-mean-of-order-r indices are increasingly used in applied economics. These indices improve upon the mean-of-order (Laspeyres, Paasche) and geometric indices without extending the information required. The quadratic mean-of-order-r indices are superlative, because they are exactly represented by flexible aggregator functions. Fundamental to this approach is the quadratic lemma.

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[6] Thus more than one index-number formula can be exact for the same aggregator function, and one index-number formula can be exact for quite different aggregator functions (Diewert 1981).

[7] Sato (1976) shows that the Vartia II indices are exact for a CES aggregator function.

Quadratic lemma—Diewert (1976a) shows that a superlative index can be expressed in terms of only first-order derivatives. This is the basic property that allows construction of quadratic mean-of-order-r indices with the same information as mean-of-order-r indices. Diewert provides a quadratic approximation lemma which uses the following homogeneous quadratic functional form:

$$f(X) = A_0 + A^T X + ½X^T AX \qquad (16)$$

$$= A_0 + {}_i\textstyle\sum_N A_i X_i + {}_i\sum_N {}_j\sum_N A_{ij} X_i X_j,$$

where A_0, A_i, and A_{ij} are constants for all i and j, X is an N-dimensional vector, and T represents the transpose operator. Diewert's quadratic approximation lemma states that if the homogeneous quadratic aggregator function f is defined by (16), then:

$$f(X^1) - f(X^0) = ½[Df(X^1) + Df(X^0)]T[X^1 - X^0], \qquad (17)$$

where $Df(X^r)$ represents the gradient vector of f evaluated at X^r, i.e., the matrix of second-order derivatives. Diewert (1981) notes that this lemma follows simply by differentiating f and substituting the partial derivatives into (17). Intuitively, the quadratic lemma states that the difference between the values of a quadratic function evaluated at two points is equal to the average of the gradient (first-order information) evaluated at both points multiplied by the difference between the points.

All first-order approximations satisfy the quadratic lemma. All second-order approximations of the form given in equation (16) also satisfy the quadratic lemma. Moreover, even quadratic functions in which the zero-order and first-order parameters are specific to a data point satisfy the quadratic lemma (the second-order terms are constant across all data points). However, should the second-order parameters be specific to a data point, then the quadratic lemma is not satisfied. Denny and Fuss (1983) provide further discussion on this point.

Contrasting Diewert's lemma with the usual Taylor's series expansion for a quadratic function indicates that knowledge of $D^2f(X^0)$, i.e., second-order terms, is not required to construct superlative indices.[8] Moreover, it is not necessary to econometrically estimate the (generally unknown) coefficients which occur in the matrix of coefficients; only the observable price and quantity vectors are required.

Due to the fundamental importance of the quadratic approximation lemma, Appendix 5 provides additional discussion. Particular attention is given to providing intuition into the lemma.

Superlative indices—An index is superlative when it is exact for an aggregator function which provides a second-order approximation to a linear homogeneous function. The superlative indices (and the quadratic mean-of-order-r aggregator function) do not require commodities to be either perfect or zero substitutes. If the relative price of a commodity increases, the economic agent decreases its use (substituting other inputs) until all marginal productivities are proportional to their new prices. Therefore, the prices from both periods or economic entities enter the superlative index to represent the marginal productivities in both periods or economic entities. Superlative indices also offer a solution to errors of aggregation (which occur because there are changes in the mix of the components making up the aggregate). Use of a superlative index-number procedure on the components of an aggregate will further capture correctly any changes or differences in the quality of the components over time or between economic entities (Christensen 1975).

Quadratic mean-of-order-r—The general class of quadratic mean-of-order-r indices are exact for the quadratic mean-of-order-r aggregator function. For $r \neq 0$, the quadratic mean-of-order-r quantity index can be written:

$$Q_r(P^0, P^1, X^0, X^1) \qquad (18)$$

$$= [{}_i\textstyle\sum_N S_i^0(X_i^1/X_i^0)^{r/2}]^{1/r}\ [{}_j\sum_N S_j^1(X_j^1/X_j^0)^{-r/2}]^{-1/r},$$

where $S_i^0 = P_i^0X_i^0/{}_i\sum_N P_i^0X_i^0$ and $S_j^1 = P_j^1X_j^1/{}_i\sum_N P_j^1X_j^1$. The quadratic mean-of-order-r price index can similarly be written:

$$P_r(P^0, P^1, X^0, X^1) \qquad (19)$$

$$= [{}_i\textstyle\sum_N S_i^0(P_i^1/P_i^0)^{r/2}]^{1/r}\ [{}_j\sum_N S_j^1(P_j^1/P_j^0)^{-r/2}]^{-1/r}.$$

A multiplicity of superlative price and quantity indices exist, depending upon the value of r. Two superlative index numbers are widely used. The Fisher Ideal index is defined for $r = 2$, and the Tornqvist index is a limiting case as r tends to 0.

Fisher's ideal—Fisher's Ideal index can be written as:

$$FI_{kl} = [(\textstyle\sum S_{li}(Z_{ki}/Z_{li}))/\sum S_{ki}(Z_{ki}/Z_{li}))]^{½}, \qquad (20)$$

where S_{li} and S_{ki} are value share weights for the two economic entities or time periods being compared (k,l), and the Z_i are the corresponding prices or quantities. This index is simply the geometric mean of the Laspeyres and Paasche indices. The Fisher Ideal index is the exact index for the linearly homogeneous quadratic mean-of-order two-aggregator function.[9] Diewert (1974b) shows that this aggregator function is flexible, implying that the Fisher Ideal index is superlative.

The Fisher Ideal index possesses several nice properties. (Diewert 1976a, 1981) The Fisher Ideal price and quantity indices can be obtained by simply interchanging the quantities and prices in the same general formula. They are also consistent with both a linear aggregator function (perfect substitution) and a Leontief aggregator function (no substitution); no other superlative index-number formula has this rather nice property. The Fisher ideal index numbers are the only pair among the quadratic mean-of-order-r numbers which satisfies the Fisher weak factor-reversal test. As a consequence, the implicit indices equal the direct indices, and no difficulty arises in choosing whether to use an implicit price or quantity index according to the relative variation in price and quantity data going from one observation to another. (See Appendices 2 and 3 for additional details.) Moreover, as the degree of data disaggregation increases (so that a quantity may become zero), the Fisher Ideal index formula remains well defined. Kirkley (1984) notes that the Fisher Ideal may be biased unless the biases inherent in the Paasche and Laspeyres exactly counterbalance one another.

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[8] Denny and Fuss (1983) generalize the quadratic lemma to the case of discrete variables. They demonstrate that the quadratic lemma can still be applied without alteration when a subset of X is a vector of noncontinuous variables. In effect, the discreteness of the variables is ignored. Denny and Fuss (1983) note that the quadratic lemma can be interpreted as resulting from a differencing of two linear approximations. They further note that the quadratic lemma is exact for linear and quadratic functions unless the latter's second-order parameters are not independent of the point of approximation. Appendix 5 discusses this latter topic in greater detail.

[9] The quadratic mean-of-order-r aggregator function f_r is defined by $f_r(Z) = ({}_k\sum_N {}_l\sum_N A_{kl} Z_K^{r/2} Z_l^{r/2})^{1/r}$. The aggregator function for Fisher's Ideal index number is therefore $f_2(Z) = (½\, {}_k\sum_N {}_l\sum_N A_{kl} Z_k Z_l)^{1/2}$, i.e., it is the square root of a homogeneous quadratic function.

Tornqvist—The Tornqvist index in its logarithmic form can be written as (Tornqvist 1936):

$$\ln TI_{kl} = \sum ½(S_{li} + S_{ki})\ln(Z_{ki}/Z_{li}), \qquad (21)$$

or, without the logarithmic transformation:

$$TI_{kl} = II_i(Z_{ki}/Z_{li})^{½}(S_{li} + S_{ki}). \qquad (22)$$

The Tornqvist index is superlative, since it is exact for the linearly homogeneous translog aggregator function.[10] The S_{ki} (revenue or cost shares) are the values of the logarithmic derivatives $Df(X^1)$ and $Df(X^0)$ of the quadratic lemma when logarithms of X^1 and X^0 (output or input quantities or prices) are used. Intuitively, the use of these shares as weights incorporates any factor substitution or product transformation which may have occurred. This index requires the assumption of constant share derivatives across comparisons k and l (Denny and Fuss 1983).

Choice among superlative indices—The choice among the various possible superlative indices, i.e., the choice of r in equation (18), for empirical applications may not be important, provided that the variation in prices and quantities is not too great going from period (or economic entity) 0 to 1 (Diewert 1981). This occurs because all superlative indices differentially approximate one other to the second order, provided prices and quantities are the same for the two periods or economic entities. Moreover, the assumption of optimizing consumer or producer behavior is not required to achieve these results. Appendix 3 provides some related discussion in this area.

Maddala (1979) suggests that differences in functional form of the aggregator function (and therefore the choice of index number) produce negligible differences in measures of TFP. Intuitively, the different functional forms suggested in the literature differ in their elasticities of substitution (which depend on the second derivatives of the production function), whereas from the quadratic approximation lemma only the first derivatives matter. Maddala suggests that for productivity measurement, other matters such as disequilibrium, measurement errors, aggregation problems, and economies of scale are more important than functional forms of the aggregator function. The choice of functional form may then be advocated for other reasons.

Denny and Fuss (1983) and Hazilla and Kopp (1984b) provide evidence that suggests caution when using the growth-accounting framework to quantify changes in productivity, outputs, and inputs, since such procedures calculated with the modern theory of index numbers ignore second-order price effects. This topic receives additional attention in Appendix 5.

Divisia indices

An alternative to approximation is the construction of Divisia indices (Deaton and Muellbauer 1980, Hulten 1973). Divisia indices analyze the continuous effects of price, quantity, or TFP changes instead of comparing two discrete price, quantity, or TFP situations. The Divisia index for period t is defined by:

$$Z(t) = Z(0)\exp[{}_0\int^{t_i} \Sigma_N S_i(t)(d\log Z_i/dt)dt], \qquad (23)$$

where $S_i(t)$ is the value share of the ith commodity defined as $S_i(t) = P_i(t)X_i(t)/{}_i\Sigma_N P_i(t)X_i(t)$ and $Z(0)$ is an arbitrary base-period (or economic entity) price, quantity, or TFP level. The Divisia index comparing, say, Z^0 and Z^1 can be written as:

$$\log(Z^1/Z^0) = {}_{Z^0}\int^{Z^1} {}_i\Sigma_N S_i d\log Z_i. \qquad (24)$$

The Divisia index is a line integral, defined with respect to infinitesimal changes in $Z_i(t)$, so that discrete approximations to the Divisia involve approximations to the continuous rate of change of components of the index and to the value share in some infinitesimal interval shares. These approximation errors could accumulate over time causing the index to drift over time. Discrete approximations to the Divisia converge to the Divisia as the discrete units of prices and quantities become small enough and if relative value shares are constant over time (or economic entities). If shares are not constant, the discrete approximation involves an error that depends on the variability of the relative shares and the length of the time period (Trivedi 1981).

Chain and fixed-base indices

Indices may be constructed using either the chain principle or the fixed-base method. The fixed-base method directly compares all changes in prices, quantities, or total-factor productivity to some initial base period or economic entity level. The base period may remain constant or may be changed after some period of time. Two overlapping series of binary comparisons using base periods can also be spliced. The chain method directly compares adjacent observations, while nonadjacent observations are only indirectly compared, using the intervening observations as intermediaries. This practice results in transitive comparisons. Frisch (1936) notes that any chain index satisfies the factor-reversal test and the circular test. Appendix 2 provides further details.

Chain indices make use of all the data from the initial year cumulated to the current year. The concept of using cumulated data leads to the Divisia index in theory and the chain index as its practical realization. In contrast, a base index provides a sequence of direct binary comparisons between the current year and the base year and no reference to the course of prices and quantities in between. Allen (1975) notes that from a statistical angle, fixed-base indices are inefficient in that they do not make full use of all the data as they unfold over time. Fixed-base indices also imply that a price (quantity) index in year t is not influenced by prices (quantities) before year t as well as those achieved in year t.

The difference between chain and fixed-base indices can be intuitively presented. The functional form of the true aggregator function is unknown, so that different index-number formulae provide first- or second-order approximations to the true underlying, but unknown, aggregator function. Approximation errors which arise with these indices are smaller, as are the changes in prices and quantities from one period to the next. These changes, and therefore approximation errors, are typically (although not always) smaller when the time periods are adjacent to one another than when separated by wide intervals.

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[10] The linearly homogeneous translog aggregator function f is defined as $\ln f(Z) = A_0 + {}_i\Sigma_n A_i \ln Z_i + ½_i\Sigma_{Nj}\Sigma_N A_{ij}\ln Z_i \ln Z_j$, where ${}_i\Sigma_N A_i = 1$, ${}_i\Sigma_N A_{ij} = {}_i\Sigma_N A_{ij} = {}_i\Sigma_N {}_j\Sigma_N A_{ij} = 0$. If input prices are being aggregated then this represents a translog unit-cost function, while if quantities are being aggregated, this represents a translog production function.

To illustrate, suppose the surface of the true aggregator function $f(X)$ is concave to the origin and smooth. Intuitively, over time a chain index "creeps along" the surface of this true aggregator function, providing in effect a piecewise approximation to this surface over the relevant range. The errors of approximation should then be relatively small. In contrast, the fixed-base index compares increasingly divergent points on the true function over time, so that the approximation errors are often increasing over time and are generally larger than with chain indices. Thus the degree of approximation should usually be closer if the chain principle rather than the fixed-base principle is used to construct index numbers. Additional intuition can be developed in terms of the quadratic approximation lemma by reference to Appendix 5, and Appendix Figure 5-1. In this case, the aproximation error with chain indices should generally be lower than with fixed-base indices because the two linear functions being averaged lie next to one another in adjacent time periods.

Errors also arise for the Paasche and Laspeyres fixed-base indices, because the base-period quantities or prices (used as weights) reflect a bundle of inputs or outputs whose composition is increasingly likely to change over time. Not a great deal of meaning can be attached to base-period indices which compare distant periods for which the relative quantities or weights may be very different. The reason why Laspeyres and Paasche index numbers (and their derivatives, the Marshall-Edgeworth and the Fisher Ideal indices) do not meet the circular test is because the weights in these indices depend on the period for which the comparisons are being made (Karmel and Polasek 1970).

Norton et al. (1985) use a fixed-base index in which the weights are not changed from period-to-period. Consequently, less information needs to be collected in order to calculate it. However, fixing the weights implies that they are increasingly out-of-date as time passes (i.e., the base-period relative prices at which outputs and inputs are being valued cease to be relevent).

Longer-term comparisons are made with chain indices by a process of chaining direct binary comparisons (also called price relatives). Such an index is called a chain index, and the formula is:

$$P_{0t}^{ch} = P_{01} \times P_{12} \times P_{23} \times \ldots \times P_{t-1,t} \tag{25}$$

where the separate links in the chain are binary comparisons between adjacent periods (two-period base indices where the base is updated each period) made according to some index-number formula. The formula reflects the basic relationship:

$$P_t/P_0 = P_1/P_0 \times P_2/P_1 \times P_3/P_2 \times \ldots \times P_t/P_{t-1} \tag{26}$$

For example, let the prices in period-0 be \$1.00, in period-1 \$1.10, in period-2 \$1.32, and in period-3 \$1.19. Then $P_{00} = 1.00$, $P_{01} = 1.10$, $P_{12} = 1.12$, $P_{23} = 0.90$, $P_{03} = 1.19$, and $P_{03} = 1.00 \times 1.10 \times 1.20 \times 0.90 = 1.19$. (Allen (1975), Frisch (1936), Karmel and Polasek (1970), Kirkley, Va. Inst. Mar. Sci., Gloucester Point, VA 23062, pers. commun. Feb. 1987).

Although the precise meaning of a chain index P_{0t}^{ch} is not simple in character, because it is based on a changing collection of items, nevertheless there is a sense in which weights are kept up-to-date in the chained index; the weights are unlikely to change radically between adjacent periods. The value of a chain index P_{0t}^{ch} will not be the same as that of a base-period index P_{0t} where a direct point-to-point comparison is involved (Karmel and Polasek 1970).

To compare prices in period 2 relative to period 1 with chain indices, either a direct binary comparison can be made (calculating the price relative to P_{12}) or a figure obtained by dividing P_{02} by P_{01}. This example is actually a specific case of the general problem of changing the base of a series. Suppose that there exists an index for a number of periods with a certain base and it is desired to change the period used as a basis for comparison. The usual practice is to divide through the whole series by the original index number for the new base. In the case of a chained index or an aggregate index with fixed weights, this correctly accomplishes the change in base. For chained indices:

$$\begin{aligned} P_{2t}^{ch} &= P_{0t}^{ch}/P_{02}^{ch} \qquad (27) \\ &= [P_{01} \times P_{12} \times P_{23} \times P_{34} \times \ldots \times P_{t-1,t}]/[P_{01} \times P_{12}] \\ &= P_{23} \times P_{34} \times \ldots \times P_{t-1}. \end{aligned}$$

In general, for two time periods s and t, where $s < t$, then the chain index between the two points P_{st}^{ch} can be defined as above, but this simply reduces to:

$$P_{st}^{ch} = P_{s,s+1} \times P_{s+1,s+2} \times \ldots \times P_{t-1,t}. \tag{28}$$

Strictly speaking, such a procedure is not valid where indices with changing weights are being used, since a change in the period of reference then requires a change in weights. In practice, this is usually ignored (Allen 1975; Frisch 1936; Karmel and Polasek 1970).

The divergency which exists between a chain index and the corresponding direct or fixed-base index (when the latter does not satisfy the circular test) will often take the form of a systematic drifting (Frisch 1936). This means that with increasing time t, the ratio P_{st}^{ch}/P_{st} $(t > s)$, where P_{st}^{ch} denotes the chain index between periods s and t, increasingly departs from unity. The Laspeyres index tends to drift upwards, the Paasche index tends to drift downwards, and the Fischer ideal index tends to drift downwards. Geometric indices should not drift over time, because there are no differences between chain and fixed-base geometric indices. Frisch notes that drifting must not be taken to mean that the fixed base index is right and the chain index wrong. Frisch (1936), Allen (1975), and Karmel and Polasek (1970) provide additional discussion and methods of measuring the amount of drifting.

Diewert (1978, 1981) generally recommends the use of chained rather than fixed-base indices. All superlative, pseudosuperlative, Paasche, and Laspeyres index numbers should coincide quite closely if they are constructed using the chain principle. The chained Paasche, Laspeyres, or any superlative index number can also be regarded as discrete approximations to the continuous-line integral Divisia index, which has some useful optimality properties from the standpoint of economic theory. These discrete approximations will be closer to the Divisia index if the chain principle is used. Moreover, the use of chained indices avoids problems of discontinuities which arise when the base year in the fixed-base indices is changed. The use of chained indices avoids the discontinuities introduced by period changes in the base year.

Consistency in aggregation

Indices of prices and quantities (input and output) and TFP might be constructed from data at the level of the individual firm or consumer (or even region or nation) or from previously constructed subindices (Deaton and Muellbauer 1980; Diewert 1978, 1981). In the first case, an index is constructed in a single step. In the second case, there are two or more stages of construction. This raises the issue of consistency in aggregation. Vartia (1974) defines an index-number formula to be consistent in aggregation if the numerical value of the index constructed in two or more stages necessarily coincides with the value of the index calculated in a single stage. Thus, for example, a discrete Divisia index of discrete Divisia indices would be the discrete Divisia index of the components. Vartia (1976a) notes that the Paasche, Laspeyres, and the geometric indices, including the Vartia I, are consistent in aggregation. Unfortunately, the superlative indices are not consistent in aggregation.

Consistent aggregation providing a perfectly satisfactory overall index that can be applied to individual periods in an intertemporal context, to individual economic entities, or to subgroups of commodities requires homothetic weak separability of the underlying aggregator function.[11] Thus to justify the two-stage method of calculating index numbers for any partition of variables requires an aggregator function, such as the Cobb-Douglas, which is homothetically separable in the same partition that corresponds to the two stages. The Paasche and Laspeyres indices are consistent in aggregation since the underlying aggregator function is either linear or Leontief, the Vartia I's underlying aggregator function is the Cobb-Douglas, and the Vartia II's underlying aggregator function is the CES. If the underlying aggregator function is not separable, any attempt to construct an overall or group quantity index by using subgroup indices will result in the group-quantity index varying with variations in quantities of commodities outside of that group. An implicitly separable underlying aggregator function for an index also allows consistent aggregation. Blackorby et al. (1978) (Deaton and Muellbauer 1978; Diewert 1978, 1981; Blackorby et al. 1978), provide further details.

Although superlative indices are not consistent in aggregation when constructing overall indices out of individual subindices, Diewert (1978) shows that they are approximately (second-order differentially) consistent in aggregation. Thus a practical objection to the use of superlative index-number formulae loses its force. Moreover, the degree of approximation will become closer if, for the time-series data, indices are constructed by chaining observations in successive periods rather than by the fixed-base method. To summarize, constructing aggregate indices by aggregating two (or more) stages will give approximately the same answer that a one-stage index would, provided that either a superlative index or the Vartia I index is used. Further, given the otherwise superior properties of the superlative index formulae, this procedure is preferred.

Homogeneity and homotheticity

The discussion of superlative index numbers has been developed in the context of aggregator functions which are linearly homogeneous. Moreover, the commodities to be aggregated are implicitly assumed to be separable. Graphically, the set of all isoquants for input quantities to be aggregated into a composite input quantity lie on a straight line from the origin and are equally spaced. The marginal rates of transformation between these inputs are therefore fixed and independent of the particular combinations of other inputs and outputs.

Should the true aggregator function (which the superlative index-number formulae approximate) be homothetic but not linearly homogeneous, then no serious difficulties arise. In the homothetic case, all isoquants (or isoproduct curves) are the same shape and, for any factor ratio, lie on a straight line emanating from the origin (the expansion path). Therefore, the distance between any pair of isoquants is the same on any ray from the origin, and bundles of inputs can be compared directly (Christensen 1975).

If the true aggregator function is nonhomothetic, then isoquants can have different shapes and do not lie on a straight line from the origin. Marginal rates of substitution (and transformation) and factor (and product) shares vary with the aggregate's level. Comparison of input (or output) bundles can be made only by reference to an isoquant corresponding to a particular level of the aggregate. Even if the true aggregator function is nonhomothetic, however, economic theory provides some appealing justification for the use of flexible index numbers. For example, Diewert (1976a) has shown that the Tornqvist index is exact for the nonhomothetic translog aggregator function when the isoquant for the geometric mean output (of the base and comparison-period input bundles) is the basis for comparison. (This is particularly appealing for multilateral indices.) Diewert (1976a) also notes that the Fisher Ideal index will indicate correctly the direction of change in the aggregate, even if the true aggregator function is nonhomothetic. Diewert (1976a, 1981) further shows that the Tornqvist and Fisher Ideal superlative index-number formulae are exact for nonhomothetic aggregator functions. In particular, he shows that any quadratic mean-of-order-r index can approximate an arbitrary nonhomogeneous function to the second order (Diewert 1976a,b, 1981; Christensen 1975; Swamy and Bingswanger 1980).

Bilateral and multilateral indices

Two basic types of output, input, and total-factor productivity (TFP) indices can be developed: bilateral and multilateral. Bilateral indices provide intertemporal comparisons of, say, TFP for any given economic entity or interspatial comparisons among economic entities for any given time period. The Tornqvist bilateral index of TFP may be written as:

$$\ln TFP_k - \ln TFP_l = \sum_i 0.5\,(R_{ik} + R_{il})[\ln Y_{ik} - \ln Y_{il}] \quad (29)$$
$$- \sum_i 0.5\,(W_{ik} + W_{il})[\ln X_{ik} - \ln X_{il}],$$

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[11] Separability is the relevant property of aggregator functions which allows aggregation. Weak separability requires that the marginal rates of technical substitution (MRTS) between all pairs of variables (e.g., prices) in a particular group of commodities be independent of changes in the levels of variables not in that group. While weak separability of the aggregator function for some group of commodities is necessary and sufficient for the existence of an aggregate, homotheticity is a necessary and sufficient condition for the validity of the multistage aggregation procedure. Homotheticity insures expansion paths for the subgroup of commodities comprising the aggregate which are straight lines emanating from the origin. Homothetic separability for the aggregate exists if the aggregator function is weakly separable in the individual components of the aggregate and the aggregator function is linearly homogeneous.

Homotheticity is a characteristic of production technology which restricts expansion paths to be straight lines from the origin. Marginal rates of substitution or transformation and factor or product shares are therefore constant along any expansion path. In contrast to homogeneity, homotheticity does not place any restrictions on the spacing of isoquants, and returns-to-scale are a function of the initial level of inputs or outputs.

where k and l are adjacent time periods (or economic entities), the Y_{ij} are output indices for output i of economic entity j, the X_{ij} are input indices, the R_{ij} are output revenue shares, and the W_{ij} are input cost shares. Diewert (1976a) shows that (29) can be derived from a homogeneous translog product-transformation function that is separable in inputs and outputs and exhibits neutral differences in technology. Caves and Christensen (1980) show that separability and Hicks neutral technological change are not required to derive (29) from a homogeneous translog product-transformation function.

The direct use of the bilateral index of TFP is limited for comparisons that are not binary, e.g., TFP of one economic entity in some time period with TFP of another economic entity of a different time period. For example, interpreting k and l as time periods or firms, the total number of possible binary comparisons of the kl time-differentiated firm observations is given by the formula for combinations. There is no guarantee of transitivity in such comparisons. As Caves et al. (1981, 1983) note, in a given year firm k might be found to be more productive than firm l and less productive than firm m; yet a direct comparison of l and m might indicate that m is less productive than l. This possible lack of transitivity occurs because weights R_{ij} and W_{ij} specific to the firms in question are used. The traditional solution to this problem is to use weights that are not specific to the individual observation. The disadvantage of this solution is that the comparisons lose what is called characteristicity, that is, they are no longer based on economic conditions specific to the two entities being compared (Caves et al. 1981, 1983).

Although transitivity of comparisons and complete characteristicity cannot be simultaneously achieved, transitive results can be achieved in a multilateral setting by the following compromise formula (Caves et al. 1982a; Caves et al. 1981, 1983):

$$\begin{aligned} \ln TFP_k - \ln TFP_l = {} & \textstyle\sum_i 0.5\ (R_{ik} + R_i^*)[\ln Y_{ik} - \ln Y_i'] \\ & - \textstyle\sum_i 0.5\ (R_{il} + R_i^*)[\ln Y_{il} - \ln Y_i'] \\ & - \textstyle\sum_i 0.5\ (W_{ik} + W_i^*)[\ln X_{ik} - \ln X_i'] \\ & + \textstyle\sum_i 0.5\ (W_{il} + W_i^*)[\ln X_{il} - \ln X_i'], \end{aligned} \tag{30}$$

where an asterisk associated with a variable indicates the arithmetic mean and an apostrophe indicates the geometric mean.[12] The use of this Tornqvist multilateral index for binary comparisons results in transitive multilateral comparisons that retain a high degree of characteristicity (revenue or cost-share weights specific to the entities and time periods). The weights used to compute the productivity comparisons reflect the economic conditions faced by all economic entities (through R_i^* and W_i^*), but at the same time more than half of each weight is specific to k or l. In effect, each economic entity is compared with all others by the multilateral index via a hypothetical entity having the geometric average characteristics of all entities. Transitive comparisons are achieved by using this representative firm as the basis for making all possible binary comparisons, i.e., any two firms are compared with each other by comparing both with the representative firm (the geometric mean).

The issue of bilateral vs. multilateral indices also applies to output and input indices. Consider outputs first. The Tornqvist bilateral output index may be written as:

$$\ln Y_k - \ln Y_l = \textstyle\sum_i 0.5\ (R_{ik} + R_{il})[\ln Y_{ik} - \ln Y_{il}], \tag{31}$$

where there are say $i = 1, \ldots, M$ outputs. The Tornqvist multilateral output index may be written as:

$$\begin{aligned} \ln Y_k - \ln Y_l = {} & \textstyle\sum_i 0.5\ (R_{ik} + i^*)[\ln Y_{ik} - \ln Y_i'] \\ & - \textstyle\sum_i 0.5\ (R_{il} + R_i \mathrm{i}^*)[\ln Y_{il} - \ln Y_i'], \end{aligned} \tag{32}$$

where the definitions are as before. Tornqvist bilateral and multilateral input indices can be derived in exactly the same manner, substituting X for Y and W for R.

Comparisons of the output and input index formulae with the TFP formula readily confirm that productivity comparisons can be interpreted as comparions of outputs to inputs.

Caves et al. (1982b) discuss the application of multilateral indices in the time-series context. Multilateral indices are applicable to cross-section data, combinations of cross-section and time-series data (panel data), and time-series data. Multilateral methods are attractive for cross-section data because there is generally no natural ordering of the data points. In contrast, time-series data have a natural chronological order. For this reason, adjacent observations in time-series data are usually directly compared, while nonadjacent observations are only indirectly compared, using the intervening observations as intermediaries. This procedure is called chain-linking, and results in transitive time-series comparisons.

Time-series comparisons using superlative bilateral chain-linked indices have the undesirable property that nonadjacent observations are only indirectly compared. Superlative multilateral indices directly compare adjacent and nonadjacent observations, but only by destroying the fixity of historical comparisons. As additional observations are added with time, expanding the set of comparisons, the chain-linked bilateral approach leaves the historical comparisons intact, but the multilateral procedure results in new comparisons for the entire time series. This occurs because the multilateral approach compares one observation with another via a hypothetical entity having the average characteristics (geometric mean) of all entities, and as observations are added over time, the hypothetical average entity changes (Caves et al. 1982a).

The choice between the bilateral and multilateral approaches depends in large part upon the importance attached to the conflicting traits of symmetry of treatment and fixity of historical comparisons. The issue of symmetry becomes important with panel data. The set of time-series comparisons could be linked together through any single cross section, but the results would differ from those obtained by choosing any other cross section. An equally unattractive alternative would construct all the cross-section comparisons and combine them by chain-linking the results through an arbitrarily chosen economic entity (firm, region). The results would then differ from those obtained by choosing any other country. The multilateral approach to panel-data comparisons treats all economic entities

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[12] Caves et al. (1981) note that the equation for Tornqvist multilateral TFP comparisons can be derived directly from a translog transformation structure by taking the difference between each firm's transformation function and the function resulting from averaging arithmetically the transformation functions across all observations. Moreover, the use of revenue shares as weights implies that the structure of production exhibits constant returns-to-scale and that the prices of the outputs are proportional to their marginal costs. Relaxation of these assumptons would require extensive econometric estimation. Finally, Caves et al. (1982a,b) note that multilateral comparisons can be obtained from Fisher Ideal bilateral indices in exactly the same way that translog multilateral indices are obtained from translog bilateral indices. However, it is not known whether or not the resulting index can be directly derived from a flexible transformation function that is nonseparable in inputs and outputs and permits non-neutral differences in productivity among economic entities. For these reasons, Tornqvist bilateral and multilateral indices are used in this study rather than the Fisher Ideal index procedure.

(firms, geographical areas) and time periods symmetrically (Caves et al. 1982a).

In conclusion, Caves et al. (1982a,b) state that the superlative multilateral indices are very attractive for cross-section and panel-data comparisons, but that they are not necessarily preferable to chain-linked bilateral indices for time-series comparisons. This follows because chronology provides a natural ordering of time-series data and historical fixity of constructed indices that is lacking for cross-section or panel data.

Productivity measurement and stock effects in marine fisheries

Intertemporal productivity measurement in marine fishing industries faces a measurement problem peculiar to all natural resource industries: variations in the composition, quantity, and quality of the natural resource being exploited. This problem exists in both renewable and nonrenewable resource industries.

In marine fishing industries, variations in the quantity and species composition of the resource stock over time affect the costs and revenue of harvesting for any given quantity of fish landed. These effects on production might in turn obfuscate the efficiency with which inputs would otherwise be converted into outputs, and could lead to biased measures of productivity. For example, fishermen might adopt fish finders which should allow them to locate and target desired species and quantities of fish while reducing search time, fuel costs, risk, spoilage, and other opportunity costs of harvesting. For any given level and species composition of fish stocks, fishermen's productivity should increase. However, if overall resource abundance is declining and lower-valued species are simultaneously increasing as a proportion, fishermen might actually have to increase their search time, fuel costs, and trip length to attain a constant revenue or catch level.

Changes in resource abundance and composition thus shift the fishery-product transformation frontier: increased resource abundance likely causes an expansion outwards, away from the origin, while decreased resource abundance likely causes a contraction of the frontier toward the origin. These shifts can either reinforce or counteract the productivity trend that would otherwise occur with a constant and homogeneous resource. The residual TFP measure might then capture resource changes along with productivity changes.

Resource changes can further and indirectly affect productivity measurement by affecting (multiproduct) economies-of-scale and capacity utilization (the latter by temporary, short-run disequilibrium). Changes in resource composition are less likely to affect TFP measurement, since induced changes in catch or effort composition should be captured by Divisia indices.

Accounting for the effects of the resource stock upon productivity measurement depends upon the approach taken toward productivity measurement. If the structural approach is adopted, a production, cost, or profit function can be econometrically estimated incorporating measures of resource abundance. Resource abundance should be interpreted as a technological constraint, since it is beyond the control of any individual firm but nevertheless affects the environment within which fishing firms operate. Changes in resource abundance may then be viewed as shifts in the technology that relate the generation of outputs to inputs. The firm's product-transformation frontier may then be written as $T(Y,X|A)$, with feasibility written as $T(Y,X|A) \leq 0$, where Y refers to a vector of outputs, X refers to a vector of inputs, and A refers to an index of technology. Resource abundance can then enter the transformation frontier as either a dummy variable or as a parameter (McFadden 1978, Daughety et. al. 1986)[13] Allowing this measure to interact with the other inputs further allows estimation of the effects of resource abundance upon economic capacity utilization and scale economies.

Current research is focusing upon incorporating the effects of resource abundance into the growth-accounting or index-number procedure. Until this research is completed, the resulting TFP measure is interpreted as not strictly the rate of technological change, but as a measure of both the technical efficiency with which inputs are converted into outputs and the effects of resource availability and composition. The TFP measure may also include changes in technical efficiency, scale effects and effects from changes in capacity utilization (which may change with changes in resource abundance and composition), and effects of public regulation possibly restricting productivity in the short run (but presumably increasing TFP over the long run as resource stocks rebuild to desirable levels).

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[13] Stollery (1985) and Halvorsen and Smith (1986) provide examples with Canadian mining. Kirkley (1986) discusses measures of fish stock abundance and production technology. Gordon (1954) first discussed resource availability as a technological constraint; Jim Kirkley (Va. Inst. Mar. Sci., Gloucester Point, VA 23062, pers. commun. Feb. 1987) first brought this to the author's attention.

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Table 1
Trawl Landings and Revenue: Washington, Oregon, northern and central California

	Pink shrimp		JV Pacific whiting		Groundfish	
Year	Tons	Revenue	Tons	Revenue	Tons	Revenue
1981	19923	20.01	48012	6.17	100414	38.06
1982	13913	13.37	74367	9.64	113492	44.33
1983	6613	8.78	79476	9.28	89538	36.71
1984	4818	3.81	86959	10.29	79938	32.26
1985	12779	7.61	34934	3.2	82988	34.86

Note: All values millions of dollars in 1981 dollars
All weights are short tons
Source: PacFIN Management database

Table 2
Number of coastwide otter and shrimp trawl vessels by region and year

Year	Wash.	Oregon	N. Calif.	C. Calif.	Total
1981	87	148	99	72	406
1982	93	169	97	69	428
1983	88	170	98	96	452
1984	97	174	80	63	414
1985	92	146	73	59	370

Note: Vessels employing both otter and shrimp trawl gear are counted only once.
Source: Annual vessel inventory and PacFIN Research database

Table 3
Total number of groundfish and shrimp landings and joint-venture weeks fished by region and year

Year	Wash.	Oregon	N. Calif.	C. Calif.	Total
1981	2488	7410	2687	2529	15114
1982	2107	7097	4181	4470	17855
1983	2302	7723	3565	3984	17574
1984	1976	6071	3441	3544	15032
1985	1908	5686	3959	4857	16410

Source: PacFIN Management database and joint-venture logbooks
Note: Excludes Puget Sound vessels

Table 4
Number of groundfish landings by region and year

Year	Wash.	Oregon	N. Calif.	C. Calif.	Total
1981	1474	4188	2062	2497	10221
1982	1570	4767	3479	4347	14163
1983	1491	6552	3500	3893	15436
1984	1615	5377	3260	3452	13704
1985	1391	4735	3761	4846	14733

Source: PacFIN Management database and Washington Dept. of Fisheries
Note: Excludes Puget Sound vessels

Table 5
Number of pink shrimp landings by region and year

Year	Wash.	Oregon	N. Calif.	C. Calif.	Total
1981	1014	3108	625	31	4778
1982	537	2082	702	75	3396
1983	811	1102	43	48	2004
1984	322	508	118	49	997
1985	488	951	171	4	1614

Source: PacFIN Management database
Note: Excludes Puget Sound vessels

Table 6
Multilateral total-factor productivity

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	0.666324	0.988394	0.878428	1.000000
1982	0.969277	0.657095	0.784490	0.780530	0.920491
1983	0.996574	0.619725	0.781322	0.672099	0.883903
1984	1.080838	0.714634	0.869972	0.808189	1.006902
1985	1.186149	0.768584	0.871066	0.737701	1.040016

Note: Tornqvist multilateral chain indices.
Normalized on either 1981 Washington or 1981 fleet.

Table 7
Bilateral total-factor productivity

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.000000	1.000000	1.000000	1.000000
1982	0.979454	0.984080	0.812086	0.905919	0.928293
1983	0.985601	0.905697	0.811335	0.762710	0.874973
1984	1.086189	0.993388	0.889217	0.919418	0.973892
1985	1.174060	1.097958	0.893955	0.836522	1.015422

Note: Tornqvist bilateral chain indices with 1981 base

Table 8
Tornqvist multilateral TFP growth rates

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	0.385915	−0.02006	0.374241	0.256295	0.232110
1982	−0.03120	−0.01394	−0.23104	−0.11816	−0.08284
1983	0.027773	−0.05855	−0.00404	−0.14956	−0.04056
1984	0.081168	0.142494	0.107473	0.184391	0.130286
1985	0.092975	0.072778	0.001256	−0.09125	0.032357
Avg.	0.042677	0.035693	−0.03159	−0.04364	0.009809

Note: Averages computed for 1982-85.
Computed following conventional productivity practice as $\ln(T+1) - \ln(T)$.
Percentages are obtained by multiplying by 100.

Table 9
Tornqvist bilateral TFP growth rates

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981					
1982	−0.02075	−0.01604	−0.20814	−0.09880	−0.07440
1983	0.006256	−0.08300	−0.00092	−0.17207	−0.05915
1984	0.097178	0.092416	0.091659	0.186863	0.107107
1985	0.077792	0.100086	0.005314	−0.09448	0.041759
Avg.	0.040117	0.023363	−0.02802	−0.04462	0.003826

Note: Computed following conventional productivity practice as $\ln(T+1) - \ln(T)$.
Percentages are obtained by multiplying by 100.

Table 10
Tornqvist multilateral-output chain indices for individual species

Year	Wash.	Oregon	N. Calif.	C. Calif.
Dover sole				
1981	1.000000	1.134581	1.235892	0.969079
1982	1.031920	1.213503	1.249156	1.014966
1983	1.043814	1.231094	1.165989	1.029052
1984	1.060182	1.165946	1.178834	1.058754
1985	1.033139	1.155265	1.243946	1.149278
Petrale sole				
1981	1.000000	1.039037	0.998366	1.007475
1982	0.995872	1.077271	0.993645	1.009050
1983	1.017418	1.058683	0.983387	0.983778
1984	1.010374	1.029645	0.990106	0.976597
1985	1.003475	1.020638	1.004848	1.005584
Other flatfish				
1981	1.000000	1.063230	1.021449	1.019490
1982	1.060928	1.080922	1.006804	1.016159
1983	1.039346	1.066653	0.997134	0.978593
1984	1.056870	1.038617	0.986737	0.966470
1985	1.072833	1.049883	1.006727	1.000616
Rockfish				
1981	1.000000	1.135445	0.845552	0.799196
1982	0.987301	1.068244	0.870419	0.960247
1983	0.921153	0.985263	0.791875	0.739806
1984	0.787059	0.940486	0.738121	0.706176
1985	0.746628	0.950586	0.780170	0.706032
Pacific cod and lingcod				
1981	1.000000	0.961548	0.944272	0.950172
1982	0.984703	0.974115	0.946402	0.949718
1983	0.988245	0.981781	0.936098	0.928333
1984	1.015783	0.965144	0.930080	0.928432
1985	1.014086	0.963693	1.013049	0.916561
Sablefish				
1981	1.000000	1.028505	1.065513	1.006452
1982	1.039216	1.061494	1.113609	1.019816
1983	1.026009	1.060395	1.069461	0.997292
1984	1.055970	1.061871	1.058095	0.998186
1985	1.001191	1.069056	1.065822	1.017845
Pacific whiting				
1981	1.000000	1.980067	3.186918	1.266354
1982		3.155684	2.200408	1.465981
1983	1.228060	3.726936	1.827943	1.891140
1984	1.829728	4.331311	1.937834	1.333818
1985	0.569838	2.575733	1.718608	1.083178
Misc. groundfish				
1981	1.000000	0.928832	0.930768	0.925377
1982	0.930179	0.921754	0.927003	0.923938
1983	0.923390	0.924609	0.926919	0.922923
1984	0.941897	0.920984	0.922016	0.921810
1985	0.931889	0.915865	0.926429	0.921569
Pink shrimp				
1981	1.000000	1.455978	0.685070	0.594482
1982	0.776709	1.039321	0.720047	0.562585
1983	0.837948	0.784123	0.537546	0.585361
1984	0.704627	0.723615	0.623711	0.466517
1985	0.918707	0.953571	0.635173	0.376092

Note: Each species normalized on 1981 Washington

Table 11
Tornqvist multilateral total-output chain index

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.291362	1.021075	0.760186	1.000000
1982	0.949664	1.316348	0.989674	0.843147	1.006640
1983	0.948678	1.301456	0.916246	0.777224	0.979096
1984	0.985571	1.337039	0.912741	0.763521	0.997392
1985	1.042698	1.306008	0.948681	0.789267	1.012015

Note: Normalized on either 1981 Washington or 1981 fleet

Table 12
Tornqvist multilateral total-output growth rates

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	0.209308	0.465006	0.230164	−0.06488	0.298703
1982	−0.05164	0.019163	−0.03123	0.103577	0.006618
1983	−0.00103	−0.01137	−0.07709	−0.08141	−0.02774
1984	0.038151	0.026973	−0.00383	−0.01778	0.018514
1985	0.056346	−0.02348	0.038620	0.033162	0.014554
Avg.	0.010453	0.002819	−0.01838	0.009385	0.002985

Note: Average computed over 1982-85.
Computed following conventional practice as $\ln(T+1) - \ln(T)$.

Table 13
Tornqvist bilateral-output chain indices for individual species

Year	Wash.	Oregon	N. Calif.	C. Calif.
Dover sole				
1981	1.000000	1.000000	1.000000	1.000000
1982	1.030778	1.046032	1.005249	1.044329
1983	1.039376	1.052024	0.919681	1.068231
1984	1.056653	1.007226	0.929270	1.116155
1985	1.032961	0.998675	0.992297	1.234016
Petrale sole				
1981	1.000000	1.000000	1.000000	1.000000
1982	0.997656	1.025436	0.996988	1.001759
1983	1.019186	1.007527	0.991650	0.972668
1984	1.011397	0.984124	0.999488	0.966593
1985	1.003844	0.976959	1.015331	1.007015
Other flatfish				
1981	1.000000	1.000000	1.000000	1.000000
1982	1.050860	1.012182	0.986576	0.993858
1983	1.035842	1.000413	0.982697	0.945585
1984	1.048375	0.980072	0.967930	0.933938
1985	1.058343	0.988099	0.988802	0.979600
Rockfish				
1981	1.000000	1.000000	1.000000	1.000000
1982	0.969789	0.963165	1.025003	1.244426
1983	0.906027	0.903112	0.942332	0.909872
1984	0.772757	0.864293	0.868502	0.881363
1985	0.738265	0.868268	0.919292	0.855615
Pacific cod and lingcod				
1981	1.000000	1.000000	1.000000	1.000000
1982	0.981546	1.008163	1.001947	0.998303
1983	0.985724	1.012166	0.994721	0.972500
1984	1.007928	0.999340	0.988133	0.976240
1985	1.001678	0.998151	1.065126	0.958621
Sablefish				
1981	1.000000	1.000000	1.000000	1.000000
1982	1.038586	1.018711	1.035889	1.011607
1983	1.025752	1.016554	0.982902	0.991006
1984	1.054688	1.016632	0.972060	0.995523
1985	0.996965	1.018245	0.979190	1.022964
Pacific whiting				
1981	1.000000	1.000000	1.000000	1.000000
1982		1.238506	0.836257	1.006033
1983	1.000293	1.288067	0.745557	1.187542
1984	1.847661	1.280507	0.768798	0.919833
1985	0.578058	1.075752	0.729935	0.918422
Misc. groundfish				
1981	1.000000	1.000000	1.000000	1.000000
1982	0.952279	0.998376	0.997840	0.998862
1983	0.946974	0.999049	0.997561	0.998054
1984	0.962312	0.998225	0.994299	0.997104
1985	0.957000	0.997644	0.996707	0.996811
Pink shrimp				
1981	1.000000	1.000000	1.000000	1.000000
1982	0.817113	0.884780	1.032789	0.961276
1983	0.843731	0.713472	0.829293	1.002105
1984	0.754689	0.688080	0.892004	0.858257
1985	0.927733	0.817190	0.899803	0.855178

Table 14
Tornqvist bilateral total-output chain index

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.000000	1.000000	1.000000	1.000000
1982	0.951994	1.017866	0.989733	1.128879	1.012927
1983	0.938590	0.981250	0.919959	1.010007	0.967034
1984	0.983368	0.957565	0.906041	1.003958	0.962535
1985	1.024315	0.966535	0.947134	1.035043	0.988344

Table 15
Tornqvist bilateral total-output growth rates

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981					
1982	−0.04919	0.017708	−0.01031	0.121225	0.012844
1983	−0.01417	−0.03663	−0.07310	−0.11126	−0.04636
1984	0.046604	−0.02443	−0.01524	−0.00600	−0.00466
1985	0.040795	0.009323	0.044356	0.030493	0.026460
Avg.	0.006006	−0.00850	−0.01357	0.008610	−0.00293

Note: Computed following conventional practice as ln $(T+1)$ − ln(T). Percentages are obtained by multiplying by 100.

Table 16
Revenue shares for individual species

Year	Wash.	Oregon	N. Calif.	C. Calif.
Dover sole				
1981	0.062378	0.090002	0.239311	0.136368
1982	0.109959	0.116553	0.262092	0.145698
1983	0.107973	0.139658	0.286786	0.188439
1984	0.137110	0.127130	0.308158	0.263875
1985	0.133598	0.133288	0.319552	0.299553
Petrale sole				
1981	0.027498	0.036147	0.024773	0.072473
1982	0.035259	0.057619	0.026134	0.067279
1983	0.057294	0.056145	0.041042	0.054172
1984	0.061184	0.043535	0.047721	0.059309
1985	0.058398	0.039441	0.054731	0.090266
Other flatfish				
1981	0.035638	0.056740	0.073943	0.175925
1982	0.085919	0.062413	0.065854	0.140396
1983	0.052500	0.064428	0.103705	0.110846
1984	0.069220	0.055251	0.083194	0.116338
1985	0.094835	0.060986	0.090399	0.141190
Rockfish				
1981	0.345909	0.258226	0.199817	0.449818
1982	0.430116	0.219123	0.254779	0.532013
1983	0.372185	0.219397	0.356498	0.407205
1984	0.273139	0.254203	0.295879	0.486615
1985	0.286877	0.294933	0.314285	0.391329
Pacific cod and lingcod				
1981	0.060677	0.016345	0.016549	0.050374
1982	0.059709	0.021286	0.019564	0.039840
1983	0.060207	0.030539	0.022901	0.019670
1984	0.087306	0.022967	0.016025	0.028949
1985	0.093287	0.023374	0.044540	0.009347
Sablefish				
1981	0.016350	0.015484	0.057081	0.037595
1982	0.052120	0.029913	0.096263	0.038811
1983	0.036808	0.035748	0.095665	0.026525
1984	0.064435	0.040548	0.084996	0.037598
1985	0.039281	0.058915	0.093637	0.064697
Pacific whiting				
1981	0.000000	0.064884	0.288935	0.000367
1982	0.000000	0.232024	0.138482	0.003749
1983	0.000143	0.298068	0.072521	0.099129
1984	0.160048	0.370051	0.099579	0.000731
1985	0.000161	0.167617	0.032845	0.000012
Misc. groundfish				
1981	0.089734	0.001264	0.003812	0.004731
1982	0.009507	0.000691	0.002876	0.004788
1983	0.001591	0.001229	0.005071	0.004764
1984	0.014890	0.000605	0.001598	0.004165
1985	0.005931	0.000252	0.003622	0.003538
Pink shrimp				
1981	0.361813	0.460904	0.095773	0.072343
1982	0.217406	0.260374	0.133951	0.027422
1983	0.311294	0.154783	0.015806	0.089246
1984	0.132663	0.085705	0.062846	0.002416
1985	0.287628	0.221189	0.046384	0.000063

Note: Columns sum to one for each year

Table 17
Revenue shares for aggregate output by region

Year	Wash.	Oregon	N. Calif.	C. Calif.
1981	0.214827	0.440626	0.241314	0.103231
1982	0.168605	0.500048	0.211973	0.119373
1983	0.223064	0.500821	0.153800	0.122313
1984	0.223811	0.474046	0.183672	0.118469
1985	0.204127	0.433124	0.218770	0.143977

Note: Rows sum to one for each year

Table 18
Revenue shares by species

Year	Flatfish	Rockfish	Sablefish	Pacific whiting	Misc. groundfish	Pink shrimp
1981	0.228841	0.282746	0.027990	0.098352	0.050674	0.311393
1982	0.274514	0.299606	0.048784	0.145825	0.032744	0.198523
1983	0.288509	0.297536	0.044072	0.172589	0.036986	0.160305
1984	0.299684	0.293630	0.053708	0.229618	0.041208	0.082149
1985	0.337891	0.311401	0.063336	0.079819	0.042878	0.164672

Note: Rows sum to one for each year

Table 19
Tornqvist multilateral-chain implicit aggregate real-output price indices

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.588297	1.100108	0.632123	1.000000
1982	0.875465	0.913271	0.940230	1.452849	0.784505
1983	1.145988	0.632382	0.650732	1.083332	0.646321
1984	0.870856	0.605587	1.119241	1.085154	0.655304
1985	0.881346	0.704910	1.265058	1.551498	0.791198

Note: Formed by Fisher weak factor-reversal test (see text for explanation). Normalized on 1981 Washington or 1981 fleet.

Table 20
Tornqvist bilateral-chain implicit aggregate real-output price indices

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.000000	1.000000	1.000000	1.000000
1982	0.864217	1.168767	0.930372	1.073803	1.055549
1983	1.146229	0.830000	0.641348	0.824957	0.870908
1984	0.863707	0.836760	1.115762	0.816667	0.891656
1985	0.887810	0.942562	1.253913	1.170751	1.032354

Note: Formed by Fisher weak factor-reversal test (see text for explanation).

Table 21
Laspeyres bilateral total-output fixed-base output index

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.000000	1.000000	1.000000	1.000000
1982	0.821997	1.153909	0.912882	1.273951	1.061186
1983	0.772182	0.910060	0.539013	1.021493	0.835867
1984	0.727997	0.760679	0.513517	0.797237	0.712299
1985	0.814834	0.786996	0.719087	0.965476	0.803519

Table 22
Paasche bilateral total-output fixed-base index

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.000000	1.000000	1.000000	1.000000
1982	0.847758	1.152493	0.909703	1.255725	1.061971
1983	0.785450	0.800268	0.537646	0.929191	0.772340
1984	0.810597	0.768892	0.559243	0.775773	0.740534
1985	0.707631	0.762588	0.695146	0.931342	0.760912

Table 23
Fisher Ideal bilateral fixed-base total-output index

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.000000	1.000000	1.000000	1.000000
1982	0.834778	1.153201	0.911291	1.264805	1.061557
1983	0.778787	0.853400	0.538329	0.974249	0.803080
1984	0.768188	0.764775	0.535893	0.786432	0.726065
1985	0.759343	0.774696	0.707016	0.948255	0.781744

Table 24
Tornqvist bilateral fixed-base total-output index

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.000000	1.000000	1.000000	1.000000
1982	0.831325	1.174962	0.906550	1.262224	1.070544
1983	0.751070	0.865508	0.513394	1.150764	0.820717
1984	2.840610	0.763753	0.544107	0.744312	1.185931
1985	0.792929	0.784339	0.666361	0.793430	0.761591

Table 25
Tornqvist multilateral-aggregate input chain index

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.938041	1.033066	0.865394	1.000000
1982	0.979766	2.003286	1.261553	1.080224	1.093590
1983	0.951940	2.100056	1.172688	1.156414	1.107696
1984	0.911859	1.870943	1.049162	0.944732	0.990555
1985	0.879063	1.699240	1.089104	1.069901	0.973076

Note: Normalized on either 1981 Washington or 1981 fleet

Table 26
Tornqvist bilateral-aggregate input chain index

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.000000	1.000000	1.000000	1.000000
1982	0.971964	1.034332	1.218754	1.246114	1.091170
1983	0.952302	1.083419	1.133882	1.324235	1.105216
1984	0.905337	0.963938	1.018920	1.091949	0.988339
1985	0.872455	0.880302	1.059488	1.237316	0.973333

Table 27
Tornqvist multilateral-aggregate input growth rate

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	−0.17660	0.485069	−0.14407	−0.32117	0.066592
1982	−0.02044	0.033111	0.199812	0.221738	0.089465
1983	−0.02881	0.047175	−0.07304	0.068155	0.012816
1984	−0.04301	−0.11552	−0.11130	−0.20217	−0.11177
1985	−0.03662	−0.09626	0.037363	0.124420	−0.01780
Avg.	−0.03222	−0.03287	0.013206	0.053034	−0.00682

Note: Average computed for 1982-85.
Computed following conventional practice as $\ln(T+1) - \ln(T)$.
Percentages obtained by multiplying by 100.

Table 28
Tornqvist bilateral-aggregate input growth rate

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981					
1982	−0.02843	0.033756	0.197829	0.220030	0.087251
1983	−0.02043	0.046365	−0.07218	0.060804	0.012789
1984	−0.05057	−0.11684	−0.10690	−0.19287	−0.11177
1985	−0.03699	−0.09076	0.039042	0.124980	−0.01529
Avg.	−0.03411	−0.03187	0.014446	0.053236	−0.00675

Note: Computed following conventional practice as $\ln(T+1) - \ln(T)$.
Percentages obtained by multiplying by 100.

Table 29
Tornqvist multilateral-input chain indices for individual inputs

Year	Wash.	Oregon	N. Calif.	C. Calif.
Capital				
1981	1.000000	1.493297	1.016260	0.712498
1982	1.164689	1.725777	1.009586	0.680118
1983	0.965152	1.731570	1.013056	0.926326
1984	1.048221	1.771869	0.806910	0.634371
1985	0.999909	1.467446	0.747832	0.594396
Labor				
1981	1.000000	2.978295	1.079983	1.016479
1982	0.846864	2.852492	1.680466	1.796623
1983	0.925241	3.104099	1.432877	1.601286
1984	0.794212	2.440112	1.383038	1.424437
1985	0.766881	2.338022	1.591238	1.952170
Fuel				
1981	1.000000	1.314194	0.924861	0.914602
1982	0.968086	1.261695	1.007578	1.022959
1983	0.984833	1.316068	0.974642	0.996861
1984	0.952958	1.198347	0.964424	0.969880
1985	0.949028	1.168710	0.994190	1.045427

Note: Normalized on 1981 Washington

Table 30
Tornqvist bilateral-input chain indices for individual inputs

Year	Wash.	Oregon	N. Calif.	C. Calif.
Capital				
1981	1.000000	1.000000	1.000000	1.000000
1982	1.141725	1.145958	0.992528	0.955572
1983	0.847359	1.003822	1.004162	1.336298
1984	1.064866	1.023683	0.803897	0.700222
1985	0.953517	0.837494	0.931737	0.938812
Labor				
1981	1.000000	1.000000	1.000000	1.000000
1982	0.846864	0.957759	1.556010	1.767497
1983	0.925241	1.042240	1.326758	1.575326
1984	0.794212	0.819298	1.280610	1.401344
1985	0.766881	0.785020	1.473390	1.920521
Fuel				
1981	1.000000	1.000000	1.000000	1.000000
1982	0.968045	0.981431	1.078369	1.108289
1983	0.983202	1.018130	1.047477	1.082092
1984	0.956085	0.916900	1.040827	1.056834
1985	0.950329	0.901658	1.070286	1.138541

Table 31

Tornqvist multilateral-aggregate input implicit real-price chain indices

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	0.908036	0.951392	0.852814	1.000000
1982	1.203309	0.603971	0.958440	1.123094	0.968105
1983	1.004202	0.512719	0.814385	1.144682	0.860481
1984	1.270734	0.561590	0.898666	0.802676	0.889275
1985	1.161675	0.539658	0.930371	1.013478	0.910484

Note: Formed by Fisher's factor-reversal test (see text for explanation).
Normalized on either 1981 Washington or 1981 fleet.

Table 32

Tornqvist bilateral-aggregate input implicit real-price chain indices

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.000000	1.000000	1.000000	1.000000
1982	1.098898	1.059757	0.898798	0.882023	1.003326
1983	0.909419	0.900371	0.763048	0.905610	0.876076
1984	1.159524	0.987504	0.838317	0.629150	0.942273
1985	1.060399	0.943734	0.866437	0.793935	0.930485

Note: Formed by Fisher's factor-reversal test (see text for explanation)

Table 33

Share of inputs in total costs

Year	Wash.	Oregon	N. Calif.	C. Calif.
Labor				
1981	0.433897	0.401721	0.435379	0.413456
1982	0.464813	0.412169	0.427663	0.375625
1983	0.466212	0.454291	0.439758	0.450216
1984	0.480218	0.465550	0.445895	0.431485
1985	0.492314	0.470206	0.443233	0.411349
Fuel				
1981	0.180059	0.225103	0.117663	0.153649
1982	0.133997	0.184159	0.157210	0.232437
1983	0.147428	0.178804	0.132978	0.148997
1984	0.109134	0.135108	0.140781	0.180984
1985	0.106073	0.145023	0.164822	0.236210
Capital				
1981	0.386043	0.373175	0.446956	0.432893
1982	0.401188	0.403670	0.415125	0.391936
1983	0.386358	0.366904	0.427262	0.400786
1984	0.410646	0.399341	0.413322	0.387529
1985	0.401612	0.384769	0.391943	0.352440

Note: Sum by column

Table 34

Share of all inputs in total costs by region

Year	Wash.	Oregon	N. Calif.	C. Calif.
1981	0.223180	0.392755	0.219352	0.164711
1982	0.218652	0.394892	0.220400	0.166055
1983	0.196351	0.399427	0.197730	0.206490
1984	0.229767	0.423828	0.188271	0.158132
1985	0.238080	0.394362	0.193572	0.173984

Note: Sum by row

Table 35

Tornqvist multilateral economic-performance chain index

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.165505	1.142894	0.651108	1.000000
1982	0.705195	0.993601	0.769585	1.009704	0.745921
1983	1.137283	0.764362	0.624313	0.636077	0.663914
1984	0.740717	0.770621	1.083505	1.092607	0.741983
1985	0.899914	1.003936	1.184420	1.293200	0.903759

Table 36

Tornqvist bilateral economic-performance chain index

Year	Wash.	Oregon	N. Calif.	C. Calif.	Fleet
1981	1.000000	1.000000	1.000000	1.000000	1.000000
1982	0.770281	1.085306	0.840614	1.102895	0.976610
1983	1.242249	0.834910	0.681934	0.694784	0.869811
1984	0.809081	0.841746	1.183507	1.193450	0.921575
1985	0.982972	1.096595	1.293736	1.233551	1.126590

APPENDIX 1

Summary of different index formulae

This appendix summarizes the most widely applied indices in order to provide an easily accessible reference of the different formulae. All indices are expressed for quantities, but extension to price indices is straightforward. Deaton and Muellbauer (1980) and Lau (1979) provide fine references. The indices compare two time periods or economic entities (firms, regions) and aggregate over $i = 1,\ldots,N$ commodities.

Paasche

$$Q_P = (X^1/X^0) = \sum P_i^1 X_i^1 / \sum P_i^1 X_i^0$$

Laspeyres

$$Q_L = (X^1/X^0) = \sum P_i^0 X_i^1 / \sum P_i^0 X_i^0 = \sum S_i^0 (X_i^1/X_i^0)$$

Tornqvist

$$Q_T = (X^1/X^0) = II_i [X_i^1/X_i^0]^{½ (S_{i1} + S_{i0})}$$

Fisher Ideal

$$Q_F = (X^1/X^0) = [\sum S_i^1 (X_i^1/X_i^0) / \sum S_i^0 (X_i^1/X_i^0)]^{½}$$

Geometric

$$Q_G = (X^1/X^0) = II_i [X_i^1/X_i^0]^{S_i}$$

Divisia

$$\ln Q_D = \ln(X^1/X^0) = \int_{X^0}^{X^1} S_i d \ln X_i$$

APPENDIX 2

Quadratic mean-of-order-*r* indices and Fisher's tests

Diewert (1976a, 1981) discusses which of Irving Fisher's tests are satisfied by the quadratic mean-of-order-*r* quantity and price indices. The quadratic mean-of-order-*r* quantity index for $r \neq 0$, $X^0 >> O_N$, $X^1 >> O_N$, $P^0 > O_N$, and $P^1 > O_N$ may be defined as:

$$Q_r(P^0,P^1,X^0,X^1) \tag{A2.1}$$

$$= [{}_i\sum_N (X_i^1/X_i^0)^{r/2} S_i^0]^{1/r} [{}_j\sum_N (X_j^1/X_j^0)^{-r/2} S_j^1]^{-/1r}$$

where $S_i^0 = P_i^0 X_i^0 / {}_i\sum_N P_i^0 X_i^0$ and $S_j^1 = P_j^1 X_j^1 / {}_j\sum_N P_j^1 X_j^1$. For $r = 2$, equation (A2.1) becomes Fisher's Ideal quantity index, while when r tends to 0, the quadratic mean-of-order-*r* index becomes the Tornqvist index as a special case. For $r \neq 0$, the (homogeneous) quadratic mean-of-order-*r* aggregator function may be written:

$$f_r(X) = [{}_i\sum_N {}_j\sum_N A_{ij} X_i^{r/2} X_j^{r/2}]^{1/r}, \tag{A2.2}$$

where $A_{ij} = A_{ji}$ for $i \neq j$.

Diewert (1976a, 1981) states that Q_r satisfies the (1) commodity reversal test, i.e., the value of the index number does not change if the ordering of the commodities is changed; (2) identity test, i.e., $Q_r(P^0,P^0,X^0,X^0) = 1$ [also $Q_r(P^0,P^1,X^0,X^0) = 1$] so that the quantity index = 1 if all quantities remain unchanged; (3) commensurability test, i.e., the quantity index remains invariant to changes in units of measurement; (4) determinateness test, i.e., Q_r does not become zero, infinite, or indeterminate if an individual price becomes zero for any $r \neq 0$ and Q_r does not become zero, infinite, or indeterminate if any individual quantity becomes zero if $0 < r \leqslant 2$ (thus the quantity indices Q_r, for $0 < r \leqslant 2$, are somewhat more satisfactory than the Tornqvist); (5) proportionality test, i.e., $Q_r(P^0,P^1,X^0,TX^0) = T$ for every $T > 0$; (6) time or point reversal test, i.e., $Q_r(P^0,P^1,X^0,X^1) Q_r(P^1,P^0,X^1,X^0) = 1$.

Define the quadratic mean-of-order-*r* price index P_r for $P^0 >> 0_N$, $P^1 >> 0_N$, $X^0 > 0_N$, $X^1 > 0_N$, for $r \neq 0$, as:

$$P_r(P^0,P^1,X^0,X^1) \tag{A2.3}$$

$$= [{}_i\sum_N (P_i^1/P_i^0)^{r/2} S_i^0]^{½} [{}_j\sum_N (P_j^0/P_j^1)^{-r/2} S_j^1]^{-1/r}$$

where S_i^0 and S_j^1 are defined as before. P_r also satisfies Fisher's tests (1) to (6).

The only Fisher tests not satisfied by the quadratic mean-of-order-*r* price and quantity indices, P_r and Q_r, are: (7) the circularity test, i.e., $P_r(P^0,P^1,X^0,X^1) P_r(P^1,P^2,X^1,X^2) \neq P_r(P^0,P^2,X^0,X^2)$, so that transitivity is not satisfied by binary comparisons[†]; and (8) the factor-reversal test, i.e., $P_r(P^0,P^1,X^0,X^1) Q_r(P^0,P^1,X^0,X^1) \neq \sum P_i^1 X_i^1 / \sum P_i^0 X_i^0$, except that P_2 and Q_2, the Fisher Ideal price and quantity indices, satisfy the factor-reversal test (so that implicit indices equal direct indices).

[†] If this test is not passed, the implication is that the price index P_{02} over the time period 0 to 2 does not depend upon how prices develop over time in the intermediate year(s), P_0 to P_2 via P_1.

APPENDIX 3

Superlative implicit indices

This appendix examines in greater detail the relationship between superlative index numbers and Fisher's factor-reversal test. It borrows heavily from Diewert (1976a, 1981) and Allen and Diewert (1981), and demonstrates that if either a price or quantity direct index is defined, then a corresponding quantity or price index can be defined implicitly by using the weak factor-reversal test [equation (13) of the text].

Define the implicit quadratic mean-of-order-r price index $P_r{}^*$ as:

$$P_r{}^*(P^0,P^1,X^0,X^1) = \sum P_i{}^1X_i{}^1/(\sum P_i{}^0X_i{}^0)(Q_r(P^0,P^1,X^0,X^1)) \tag{A3.1}$$

and the implicit quadratic mean-of-order-r quantity index $Q_r{}^*$ as:

$$Q_r{}^*(P^0,P^1,X^0,X^1) = P_i{}^1X_i{}^1/(\sum P_i{}^0X_i{}^0)(P_r(P^0,P^1,X^0,X^1)) \tag{A3.2}$$

Thus implicit quadratic mean-of-order-r indices defined in this manner will satisfy the weak factor-reversal test of Fisher, equation (13). Then $(P_r{}^*,Q_r)$ and $(P_r,Q_r{}^*)$ are both superlative pairs of index-number formula. However, this is not necessarily so for the pair of direct superlative indices (P_r,Q_r).

The Fisher Ideal index, where $r = 2$, does satisfy the weak factor-reversal test. Therefore, $P_2(P^0,P^1,X^0,X^1)Q_2(P^0,P^1,X^0,X^1) = \sum P_i{}^1X_i{}^1/\sum P_i{}^0X_i{}^0$, (P_2,Q_2) is a pair of superlative indices, and $(P_2,Q_2{}^*) = (P_2{}^*,Q_2) = (P_2,Q_2)$.

The Tornqvist index, where r tends to 0, does not satisfy the weak-factor reversal test in general, i.e., $P_0(P^0,P^1,X^0,X^1)Q_0(P^0,P^1,X^0,X^1) \neq \sum P_i{}^1X_i{}^1/\sum P_i{}^0X_i{}^0$. This occurs because the quantity index Q_0 is consistent with a homogeneous translog aggregator function, while the price index P_0 is consistent with an aggregator function which is dual to the translog unit-cost function, and the two aggregator functions do not in general coincide. They instead correspond to different (aggregation) technologies, i.e., they are not self-dual. Thus, given Q_0, the corresponding price index, which satisfies the weak factor-reversal test, is the implicit index defined by $P_0{}^*(P^0,P^1,X^0,X^1) = \sum P_i{}^1X_i{}^1/(\sum P_i{}^0X_i{}^0)[Q_0(P^0,P^1,X^0,X^1)]$. Alternatively, given P_0, the corresponding quantity satisfying the weak factor-reversal test is the implicit index defined by $Q_0{}^*(P^0,P^1,X^0,X^1) = \sum P_i{}^1X_i{}^1/(\sum P_i{}^0X_i{}^0)[P_0(P^0,P^1,X^0,X^1)]$. The price-quantity indices P_0, $Q_0{}^*$ correspond to a translog unit-cost (or revenue) function, while $P_0{}^*$, Q_0 correspond to a homogeneous translog aggregator function.

The price-quantity index pair $(P_0, Q_0{}^*)$ is advocated by Kloek (1967) over the pair $(P_0{}^*, Q_0)$. He argues that as data and the level of study are increasingly disaggregated, the individual consumer or producer will utilize positive amounts of fewer and fewer goods (i.e., as N grows, components of the vectors X^0 and X^1 will tend to become zero), but the prices which the producer or consumer face are generally positive irrespective of the degree of disaggregation. Since the logarithm of zero is not finite, Q_0 will tend to be indeterminate as the degree of disaggregation increases, but P_0 will still be well defined (provided that all prices are positive).

The choice between $(P_r, Q_r{}^*)$ and $(P_r{}^*, Q_r)$ can alternatively be made by comparing the variation in the N-quantity ratios $(X_i{}^1/X_i{}^0)$ to the variation in the N-price ratios $(P_i{}^1/P_i{}^0)$. If there is less variation in the price ratios than in the quantity ratios, i.e., prices are more highly proportional than quantities, then the various types of direct superlative price indices P_r are essentially share-weighted averages of the price ratios $(P_i{}^1/P_i{}^0)$, and will tend to be in closer agreement with each other than the implicit price ratios $P_r{}^*$. In this case, the aggregates generated by direct-price indices should all be numerically close (and they can be approximately justified using Hick's Aggregation Theorem). Thus in this situation, use of a superlative direct-price index and the corresponding implicit-quantity index, $(P_r, Q_r{}^*)$, is preferred for some r (Allen and Diewert 1981).

If there is less variation in the quantity ratios than in the price ratios, then the direct quantity indices Q_r are essentially share-weighted averages of the quantity ratios and will tend to be more stable than the implicit-quantity indices $Q_r{}^*$. Use of a direct superlative-quantity index Q_r and corresponding implicit-price index P_r may be preferable for some r, and the aggregates generated by these indices should all be numerically close (and can be justified by Leontief's Aggregation Theorem) (Allen and Diewert 1981).

Allen and Diewert (1981) present a simple procedure by which to empirically determine whether prices are more highly proportional than quantities. They suggest individually regressing $\ln(P_i{}^1/P_i{}^0)$ and $\ln(X_i{}^1/X_i{}^0)$ on constants. The sum of squared residuals of the regressions (SSR) will then be measures of nonproportionality of the vectors P^0 and P^1 and X^0 and X^1, respectively. Prices are then less proportional than quantities if the SSR from the price-ratio regression is greater than the SSR from the quantity-ratio regression. In this case, the use of the superlative index-number pair $(P_r{}^*, Q_r)$ for some r is recommended in order to aggregate the data. If the converse holds, then the superlative index-number pair $(P_r, Q_r{}^*)$ for some r is recommended.

If the proportionality criterion cannot distinguish whether prices are more proportional than quantities, Fisher's Ideal index may be preferred since $P_2 = P_2{}^*$ and $Q_2 = Q_2{}^*$ (and thus the formula is approximately consistent with both Hick's and Leontief's aggregation theorems). Moreover, the Fisher Ideal index also lies between the Paasche and Laspeyres indices, since it is the geometric mean of the Paasche and Laspeyres indices.

Tornqvist indices are preferred over Fisher Ideal indices if multilateral indices are employed, since to date it is not known whether or not Fisher Ideal multilateral indices can be directly derived from a flexible transformation function that is nonseparable in inputs and outputs and permits non-neutral differences in productivity among economic entities, while this has been demonstrated for the Tornqvist multilateral index by Caves et al. 1981. Moreover, because the data for this study are available in quantity and revenue values, the Tornqvist implict index for prices and the Tornqvist direct index for quantities, $(P_0{}^*, Q_0)$, is used.

APPENDIX 4

Aggregation of outputs

Aggregation of individual outputs into a composite output is accomplished by a factor-requirements function for quantities and a unit-revenue function for prices. A factor-requirements function relates the minimum amount of aggregate input required to produce the vector of outputs, while the unit-revenue function provides the maximum amount of total revenue for a given level of an aggregate input. Kirkley (1986) provides additional theoretical background on revenue functions.

The quadratic mean-of-order-*r* functional form can be used to provide superlative price and quantity indices by aggregating individual prices and quantities, respectively. For example, the linearly homogeneous translog functional form provides a second-order approximation to an arbitrary twice-differentiable factor-requirements function:

$$\ln Y = A_0 + {}_i\Sigma_M A_i \ln Y_i + ½\ {}_i\Sigma_M\ {}_j\Sigma_M A_{ij} \ln Y_i \ln Y_j, \qquad \text{(A4.1)}$$

where ${}_i\Sigma_M A_i = 1$, ${}_i\Sigma_M A_{ij} = {}_j\Sigma_M A_{ij} = {}_i\Sigma_M\, {}_j\Sigma_M A_{ij} = 0$, and the producer is producing M outputs, $Y = (Y_1, Y_2, \ldots, Y_M)$.

The Tornqvist output quantity index may then be specified as:

$$g(Y^1)/g(Y^0) = {}_i\Pi_M [Y_i^1/Y_i^0]^{½}(S_i^1 + S_i^0), \qquad \text{(A4.2)}$$

where $S_i^1 = P_i^1 Y_i^1 / \Sigma P_i^1 Y_i^1$ and $S_i^0 = P_i^0 Y_i^0 / \Sigma P_i^0 Y_i^0$.

Similarly, if the unit-revenue function $R(P)$ is translog over the relevent range of data and the producer is maximizing revenue, the Tornqvist product-price index can be defined as:

$$R(P^1)/R(P^0) = {}_i\Pi_M [P_i^1/P_i^0]^{½}(S_i^1 + S_i^0), \qquad \text{(A4.3)}$$

which in log form becomes:

$$\ln(P^1/P^0) = {}_i\Sigma_M ½(S_i^1 + S_i^0)\ln(P_i^1/P_i^0). \qquad \text{(A4.4)}$$

Diewert (1974a, 1976a) provides additional details, including the dual theoretical relationship between revenue functions and factor requirement functions.

APPENDIX 5

Quadratic approximation lemma

Denny and Fuss (1983) provide intuition into the quadratic approximation lemma given in equation (17). In particular, they show that the quadratic lemma of Diewert (1976a) can be interpreted as resulting from a differencing of two linear approximations. The discussion in this appendix follows their discussion quite closely.

Consider the true aggregator function $Y = f(X)$, where $X = (X_1, X_2, \ldots, X_N)$. with mth-order continuous partial derivatives with respect to the X_i. $Y = f(X)$ can then be approximated by an mth-order Taylor-series expansion around the point X^r:

$$Y = Y_r + \Sigma_i f_i^r [X_i - X_i^r] + (½!)\ \Sigma\Sigma_{ij} f_{ij}^r [X_i - X_i^r]$$
$$[X_j - X_j^r] + \ldots + (1/m!)\ i,j,\ldots,m=1,\ldots,N\ f_{ij\ldots m,r}$$
$$[X_i - X_{ir}][X_j - X_j^r] \ldots [X_m - X_{mr}] + R_{m+1}{}^r, \qquad \text{(A5.1)}$$

where $R_{m+1}{}^r$ is the $(m+1)$-order remainder term and the superscript r denotes evaluation at r.

Replace X_i by X_i^s. Then the right-hand side of the Taylor-series expansion is just equal to Y^s. If the roles r and s are reversed (i.e., evaluate the derivatives at s and replace X_i^r by X_i^s and X_i by X_i^r), an expression is obtained for Y^r. Subtracting the two expressions and dividing by 2 provides an exact representation of the difference $Y^s - Y^r$. This difference, with suitable interpretation, is the general growth-accounting equation.

Consider now a linear approximation to the true aggregator function $Y = f(X)$ and that two data points are observed, $\{X_r\}$ and $\{X^s\}$. These data points and the corresponding true values of the true aggregator function, Y^r and Y^s, are labelled A and B in Appendix Figure A5.1 (again, adapted from Denny and Fuss 1983).

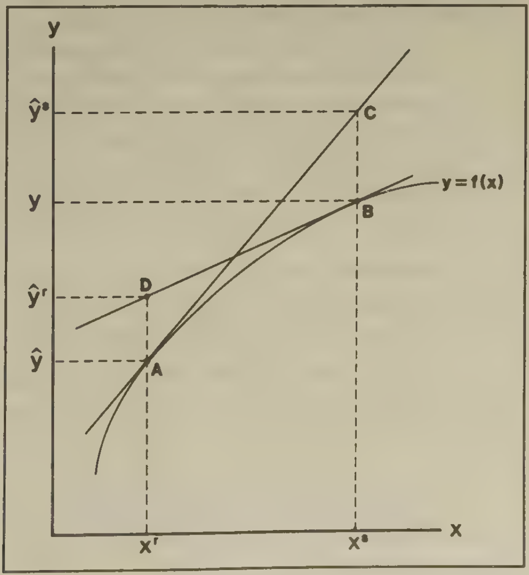

Figure A5.1
Quadratic approximation lemma.

It is assumed that the true function $f(X)$ is unknown and hence Y^s and Y^r and the difference $Y^s - Y^r$ are also unknown.

To approximate Y^s, take a linear approximation of $f(Y)$ around A and evaluate it at X^s. This point is called C and the corresponding value on the vertical axis, Y^{*s}. The approximation can be written as:

$$Y^{*s} = Y^s - R_2^s = Y^r + \sum_i f_i^r\,[X_i^s - X_i^r]. \qquad \text{(A5.2)}$$

Similarly, to approximate Y^r, take the linear expansion of $f(X)$ around B and evaluate it at X^r, denoting the point D and the relevent value Y^{*r}. This approximation can be written as:

$$Y^{*r} = Y^r - R_2^s = Y^s + \sum_i f_i^s\,[X_i^r - X_i^s]. \qquad \text{(A5.3)}$$

The unknown difference $Y^s - Y^r$ can be approximated by the approximate difference $Y^{*s} - Y^{*r}$, where:

$$\begin{aligned} Y^{*s} - Y^r &= (Y^s - Y^r) + (R_2^s - R_2^r) \qquad \text{(A5.3)} \\ &= (Y^r - Y^s) + \textstyle\sum_i [f_i^r + f_i^s][X_i^s - X_i^r]. \end{aligned}$$

Utilizing the last set of equalities and solving for $Y^s - Y^r$ provides:

$$\begin{aligned} Y^s - Y^r = {} & 0.5\textstyle\sum_i [f_i^r + f_i^s][X_i^s - X_i^r] \qquad \text{(A5.4)} \\ & + 0.5[R_2^r - R_2^s]. \end{aligned}$$

By ignoring the error of approximation $0.5[R_2^r - R_2^s]$, this last equation becomes the quadratic approximation lemma.

All first-order approximations satisfy the quadratic lemma. All second-order approximations of the form given in equation (16) also satisfy the quadratic lemma. Moreover, even quadratic functions in which the zero-order and first-order parameters are specific to a data point (e.g., s) satisfy the quadratic lemma. However, should the second-order parameters be specific to a data point, then the quadratic lemma is not satisfied.

APPENDIX 6

Constructing index numbers on electronic spreadsheets with personal computers

This appendix suggests ways of constructing Tornqvist chain index numbers on electronic spreadsheets using personal computers. After the data is placed on a spreadsheet (e.g., LOTUS), create a table composed of only the share-weighted binary logarithmic changes from time-period to time-period. Unfortunately, the relative copy command of LOTUS cannot be used to make copies of a general formula. These numbers are binary period-to-period changes. Next, create a second table composed of the exponents of the logarithmic changes. The copy command of LOTUS can be used to create this table. This table represents the Tornqvist binary index numbers for period-to-period changes, that is, as if the base period is updated with each time period.

To create chain indices, create a third table in the electronic spreadsheet. Index the intial time period 0, the second time period 1, the third time period 2, and so forth. Then the value of the chain index in time T is simply $P_{0T}^{chain} = P_0 \times P_{01} \times P_{12} \times \ldots \times P_{T-1,T}$. Thus the value of the chain index in period 1 is simply the value of the first period's binary index P_{01} (from the second of the created tables) multiplied by the initial base-period value P_0. The value of the chain index in period 2 is then the value of the second period's binary index P_{12} (from the second of the tables created) multiplied by the product $P_0 \times P_{01}$, which is the value of period 1's chain index and which has already been created in the third table (the one currently being worked in). Once a single column of chain indices has been created, the relative copy command can then be used for other economic entities if more than one is being analyzed.

The initial base-period value P_0 differs, depending upon whether or not a bilateral or multilateral index is constructed. The base-period value for a bilateral index is simply 1.0. The base-period value for a multilateral index is the logarithmic change of the base period not from a preceeding period as created in the first of the three tables, but from the geometric mean. This value for an output index of a single species is simply $0.5(R_{i0} + R_i^*)(\ln Y_{i0} - \ln Y_i')$; for a single input it becomes $0.5(W_{j0} + W_j^*)(\ln X_{j0} - \ln X_i')$; and for total-factor productivity it is simply the difference between these two, where R indicates a revenue share, W indicates a cost share, * indicates the arithmetic mean, ′ indicates the geometric mean, Y indicates output, X indicates input, and ln indicates natural logarithm. These logarithmic changes are placed in the first table created (which is composed of binary, share-weighted period-to-period changes). Because of the interpretation of the first period as deviations from the geometric mean, the initial period's revenue ratio used in Fisher's factor-reversal test used to construct implicit indices is the initial period's revenue to the arithmetic mean of all revenues.

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Production technology, costs, and multiproduct industry structure: an application of the long-run profit function to the New England fishing industry

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Abstract. The long-run multiproduct profit function is developed to provide a more general procedure than the static minimum cost function to examine the technological and cost determinants of multiproduct industry structure and the likely form of any market equilibrium. In this approach outputs are endogenous and the long-run equilibrium levels of quasi-fixed factors are endogenously determined. The multiproduct structure of the multispecies New England fishing industry and the likely multiproduct form of any open-access equilibrium are examined.

Technologie de production, coûts, et structure industrielle à plusieurs produits: une application de la fonction de profit de longue période à l'industrie des pêches de la Nouvelle Angleterre. L'auteur développe la fonction de profit de longue période pour une industrie où les firmes produisent plusieurs produits afin de mettre en place un cadre d'analyse plus général que la fonction de coûts minima en statique. Cela lui permet d'examiner les déterminants (côté coûts et côté technologie) de la structure industrielle à plusieurs produits et la forme plausible de l'équilibre de marché susceptible de s'ensuivre. Dans cette approche, les niveaux de production sont endogènes et les niveaux de facteurs de production quasi-fixes en équilibre de longue période sont déterminés de façon endogène. L'auteur examine la structure à plusieurs produits de l'industrie des pêches de plusieurs espèces de la Nouvelle Angleterre et la forme multi-produits plausible que l'équilibre est susceptible de prendre quand l'accès est libre.

The multiproduct firm's structures of costs and technology are important determinants of multiproduct industry structure. In order to analyse this structure, Baumol, Panzar, and Willig (1982) recently established theoretical conditions for the existence of multiproduct cost advantages that can be achieved by specialized or diversified firms according to the scale and scope of their production. MacDonald and Slivinski (1985, 1987) further developed the

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analysis of multiproduct industry structure through a multiproduct generalization of Viner's (1952) procedure. In this approach costs are primarily distinguished between fixed and variable, upon which various forms of structure can be placed. The primary issue then becomes the existence of specialized and diversified firms in specialized, diversified, or mixed market equilibriums due to an advantage in either variable or fixed costs.

The theoretical treatments of MacDonald and Slivinski and Baumol, et al., do not necessarily require firms to produce the same exogenously specified set of goods; that is, a firm's product combinations can be endogenous although the overall industry level is exogenous. Yet, empirical analyses of multiproduct industry structure have typically used static minimum cost functions to examine these technological and cost determinants, and this approach implicitly assumes that each firm's outputs are exogenously determined and inputs are in full static equilibrium. (For recent examples, see Gillen and Owen, 1984; Mayo, 1984; and Kohli, 1981.) Both of these conditions are likely to be violated in practice, and any subsequent analyses of multiproduct industry structure and form of equilibrium are likely to be biased. Empirical analysis should therefore allow both for outputs to be decision variables to firms and for empirical determination of the long-run equilibrium levels of any quasi-fixed factors. A ready distinction between variable and fixed costs would also be more consistent with the theoretical treatments. The long-run multiproduct profit function offers just such a general approach to provide analyses consistent with theoretical conditions.

The long-run multiproduct profit function is developed in this article to analyse the firm-level technological and cost determinants of the multispecies New England otter trawl industry's structure and to determine the likely form of an open-access equilibrium.[1] Although Gordon (1954) first posited the general principles of an open-access equilibrium in fishing industries, its detailed multiproduct form at the level of the individual firm has been neglected.

The structures of the New England and many other coastal fishing industries have remained largely composed of single-vessel firms individually owned and operated. While many U.S. industries have become structurally concentrated through firm amalgamation, most of the fishing industries have displayed little vertical or horizontal integration. This structure has persisted despite the Magnuson Fisheries Conservation and Management Act (hereafter the Magnuson Act) of 1976 and the United Nations Third Law of the Sea Conference, which extended economic zones to 200 miles and severely curtailed the previously dominant fishing of foreign distant-water fleets. Rather than expanding to the larger scale but narrower scope of the foreign fleets, which might have allowed domination of the newly protected industries, the United

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[1] Otter trawling involves dragging a net at the stern or side of a vessel. After a period of time, the net is hauled in and its catch released onto the deck, where it is sorted, gutted, and packed in ice. The process is repeated throughout the fishing trip.

States and many other coastal nations have largely maintained their scope of production but with limited scale.

This paper thus develops the long-run multiproduct profit function and several long-run multiproduct cost concepts for the profit function to explain the persistent atomistic structure of the New England otter trawl industry, the prevalence of individual ownership and operation of single-vessel, multiproduct firms, the likely form of any open-access multiproduct equilibrium, and the failure of New England vessels to increase their scale of production to that of foreign distant-water fleets after the Magnuson Act. The paper is organized as follows. The next section discusses the long-run multiproduct profit function, while the third section develops the long-run multiproduct cost concepts. The fourth section provides an industry background, and the fifth section empirically implements the model. The sixth section provides the empirical results, and concluding remarks follow in the last section.

LONG-RUN PROFIT FUNCTION

The long-run multiproduct function is developed from the restricted (or variable) profit function. The restricted profit function HR may be defined as: $\mathrm{HR}(P_M, P_N; K) = [\max_{Y,X} P'_M Y - P'_N X:(X, Y; K) \in Z]$, where HR is restricted profit (total revenue less variable costs), P_M is an $M \times 1$ vector of output prices, P_N is an $N \times 1$ vector of variable factor prices, $P = (P_M, P_N)$, $'$ is the transpose operator, Y is an $M \times 1$ vector of outputs, X is an $N \times 1$ vector of variable factors, K denotes the level of the quasi-fixed factor, capital, and Z represents the restricted production possibilities set for which a number of regularity conditions are assumed (McFadden, 1978). Given the assumptions on Z, HR is non-negative and well defined for all $P > 0$ and any K, HR is continuous, linearly homogeneous, and convex in P, HR is continuous, non-decreasing, and concave in K, and HR is non-decreasing (non-increasing) in $P_M(P_N)$ for every fixed K (McKay, et al.). Total profit, HT, at K can be specified as $\mathrm{HT}(P, K) = \mathrm{HR}(P; K) - P_K K$, where P_K is the market rental (service) price of capital.

The long-run multiproduct profit function, H, is obtained by application of the envelope condition (Samuelson, 1953). This condition states that in static equilibrium, the derivative of HR with respect to the quasi-fixed or fixed factor – that is, the shadow price – must equal the market rental price: $P_K = \mathrm{HR}_K (P, K^*)$, where HR_K is the first partial derivative of the restricted equilibrium profit function with respect to K (or the shadow price of capital), and K^* is the optimal stock of capital. Optimal long-run levels of demand for K are obtained by solving $P_K = \mathrm{HR}_K(P, K^*)$. Substitution of K^* into total profit provides the long-run multiproduct profit function in terms of P and $K^*: H(P, P_K) = \mathrm{HR}[P, K^*(P, P_K)] - P_K K^*(P, P_K)$.

MULTIPRODUCT COST CONCEPTS

The restricted profit function embodies information not only on the firm's long-run technology, but also on the firm's cost structure.[2] This is easily shown by equivalently writing HR(·) as $\text{HR}(P_M, P_N; K) = [\max_Y P'_M Y - C(P_N, Y; K)]$, where $C(P_N, Y; K)$ is the firm's restricted cost function (Sakai, 1974). Hence firms initially minimize variable costs for each level of output conditional on the level of K and then maximize restricted profits conditional on K. Note that Y is a decision variable to firms. The long-run profit function, H, at K^* becomes $H(P, P_K) = \text{HR}[P, K^*(P, P_K)] - P_K K^*(P, P_K) = [P'_M Y^* - C(P_N, Y^*, K^*) - P_K K^*(P, P_K)]$, where Y^* is optimal Y. In contrast, the static minimum cost function is specified: $C(P_N, P_K; Y)$, where Y is exogenous. Evaluating the structure of long-run multiproduct costs from the long-run profit function rather than the static minimum cost function insures that evaluation is at optimal Y and K rather than the presumed K and an exogenous level and mix of Y which may or may not be optimal.

Economies of scope

Economies of scope are one of the most important elements of the multi-product cost structure and measure the effects of joint production upon costs. Economies of scope can arise from two cost sources: weak cost complementarity and fixed costs (Gormon, 1985). A twice differentiable multiproduct cost function C exhibits weak cost complementarities over the product set M, up to Y, if $C_{ij}(Y'') \leqq 0$, i not equal to j, for all Y'' with $0 \leqq Y'' \leqq Y$, with the inequality holding strictly over a set of non-zero measure, where C_{ij} is the second partial derivative of C with respect to products i and j. Thus the marginal cost of producing one product decreases (weakly) with increases in the quantities of all other products (Baumol, et al., 1982). In the absence of fixed costs, weak cost complementarities are a sufficient condition for economies of scope (Baumol, et al., 1982). In the absence of weak-cost complementarities, fixed costs can also generate scope economies. Fixed costs can also overcome weak-cost discomplementarities to generate economies of scope (Gormon, 1985).

The presence of weak-cost complementarities can be determined from the long-run multiproduct profit function by the results of Sakai and Lau (1976). Sakai indicates the following relationship between the Hessian matrix of C and the Hessian of the profit function H: $[C_{ij}] = [H_{ij}]^{-1}$, $i \neq j$, $i, j \in M$, where H_{ij} represents the second partial derivative of H with respect to the ith and jth product prices. Lau relates the derivatives of the long-run (H) and restricted (HR) profit functions, so that all terms entering $[H_{ij}]^{-1}$ can be derived from the restricted profit function:

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[2] The cost or profit function summarizes all economically relevant information about the production technology of the firm but not about the firm's organizational technology. As Teece (1980) notes, to assert otherwise would involve assuming rather than deducing the condition for efficient multiproduct organization.

$$H_{ij} = \mathrm{HR}_{ij} - (\mathrm{HR}_{KK})^{-1}\mathrm{HR}_{iK}\mathrm{HR}_{jK}, \qquad i, j \in M. \tag{1}$$

Product-specific returns to scale

Product-specific returns to scale measure the change in costs through variation in the output of one product while holding the quantities of other products constant. Firms with increasing product-specific returns to scale have a cost incentive to expand the scale of production of this product and may become specialized in its production. Following Baumol et al. (1982), define incremental cost of product i at Y as: $\mathrm{IC}_i(Y) = C(Y_i) - C(Y_{M-i})$, where Y_{M-i} is the output vector in which $Y_i = 0$. Average incremental costs at Y are $\mathrm{AIC}_i(Y) = \mathrm{IC}_i(Y)/Y_i$. Product-specific economies of scale at Y, $S_i(Y)$, are $S_i(Y) = \mathrm{IC}_i(Y)/Y_iC_i = \mathrm{AIC}_i(Y)/C_i$, where C_i is the marginal cost of C with respect to product i. S_i at Y are increasing, decreasing, or constant as $S_i(Y)$ is greater than, less than, or equal to unity, respectively.

The profit function cannot directly measure product-specific returns to scale, but a sufficient condition can be obtained by examining incremental marginal costs (Baumol, et al., 1982). The diagonal elements of the Hessian submatrix for outputs provide the measure of incremental marginal costs: $H_{ii}^{-1} = C_{ii}(P_N, P_K, Y^*)$. $H_{ij}^{-1}(Y^*) < 0$ implies decreasing marginal and average incremental costs, $S_i(Y^*) > 1$, and marginal costs from $i >$ revenue from i. Because the inverse marginal cost curves $C_i(P_N, P_K, Y^*)^{-1}$ equated to product prices are synonymous with the product supply curves at Y_i^* (Beattie and Taylor), a direct relationship exists between the firm's product supply and marginal cost curves with the profit function – in contrast to the minimum cost function.

Long-run multiproduct returns to scale

Long-run multiproduct or ray returns to scale for the profit function measure the behaviour of costs for proportional changes in total firm output and all variable and fixed inputs.[3] This is a straightforward extension of the concept of single-product scale economies, where the output composition remains fixed while its scale can vary. The degree of long-run ray returns to scale equals the ratio between long-run production costs and the revenues that occur with marginal cost pricing. The revenues exceed, are less than, or equal long-run costs as there are decreasing, increasing, or locally constant long-run ray returns to scale (Bailey and Friedlaender, 1982).

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[3] The single-product profit function is not well defined for increasing or constant returns to scale, but the multiproduct profit function does not suffer from this limitation. The structure of multiproduct costs is dependent upon both the scale and the composition of outputs. Increasing ray returns to scale implies only that the existing division of products among more than one firm would be more costly than monopoly production. Some other division of outputs among smaller, perhaps specialized, firms may provide an even less costly form of organization. Moreover, the profit function can still be estimated if firms are not price takers. (Diewert, 1982)

Cost subadditivity

The concept of cost subadditivity provides an additional measure by which to characterize the multiproduct cost structure. A cost function is said to be subadditive at an output vector, say Y, if and only if it is cheaper for a single firm to produce Y than to split it among more than one firm in any fashion. Formally, a cost function C is strictly subadditive at Y if $C(Y) < {}_i\Sigma_k C(Y_i)$ whenever ${}_i\Sigma_k Y_i = Y$ (Baumol et al., 1982).

The presence of cost subadditivity would suggest that some form of fishermen's monopoly is appropriate on private efficiency grounds. The monopoly could be private, could entail either complete government ownership and control as is found in the socialist block nations, could include extensive government co-ordination and regulation as is found in north-east Asia, or could consist of a set of single-product firms contracting among themselves.

Tests of cost subadditivity are difficult to devise, since one of the requirements is global knowledge of the cost function, while local knowledge in the neighbourhood of the point of approximation is usually the best that can be achieved. Acceptance of local subadditivity then provides a sufficient condition for global cost subadditivity (Evans and Heckman, 1984). Although Baumol et al. (1982) provide both necessary and sufficient conditions for cost subadditivity, the long-run multiproduct profit function (and cost function) allows only local sufficient conditions. Failure to establish cost subadditivity will then not preclude its existence. Previous tests of cost subadditivity specify all factors of production to be in full static equilibrium and outputs as exogenously fixed – specifications relaxed in this study.

In general, cost subadditivity requires economies from proportional expansion of the product vector along an output ray and economies arising from product combinations along a cross-sectional hyerplane (Baumol, et al., 1982). A necessary and sufficient condition for economies from proportional expansion of products along a ray is ray subadditivity.[4] Increasing multiproduct returns to scale up to Y in turn imply decreasing average costs along a product ray (ray average cost) up to Y, and therefore ray subadditivity at Y (Baumol, et al., 1982).[5]

Sufficient conditions for cross-sectional economies include the existence of cost convexity, weak cost complementarity throughout the product set, or transray convexity. Cost convexity and weak cost complementarity are sufficient conditions for transray convexity (Wang Chiang, 1981). Roughly speaking, a cost function is transray convex if, as a firm changes the composition of output while holding fixed the level of some aggregate measure for output, costs will be lower for diverse rather than specialized output mixes

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[4] A cost function C is strictly ray subadditive at Y if, for any set of two or more positive numbers v_i that sum to one, $C(v_i Y) > C(Y \Sigma v_i) = C(Y)$ (Baumol, et al., 1982)

[5] Ray average costs (RAC) of producing the output vector Y are given by RAC $= C(kY)/k$, where Y is the vector of firm outputs, arbitrarily set equal to unity, and k is a positive constant. This defines the behaviour of costs along a ray emanating from the origin. RAC are said to be declining (increasing) as $C(k_1 Y)/k_1 < (>)\ C(k_2 Y)/k_2$ for $k_1 > k_2$ (Mayo, 1984).

(Bailey and Friedlaender, 1982).[6] Overall transray behaviour is difficult to test with either cost or profit functions, but testing for pairwise transray convexity is straightforward. If transray convexity does not exist among all product pairs, then transray convexity does not hold (Wang Chiang, 1981). Baumol et al. (1982) indicate that either one of the following conditions is sufficient for transray convexity between outputs i and j:

$$C_{ii} \geqq 0,\ C_{jj} \geqq 0,\ C_{ij} = C_{ji} \leqq 0,$$

$$C_{ii} \leqq 0,\ C_{jj} \leqq 0,\ C_{ij} = C_{ji} \leqq 0,\ C_{ij} \leqq -(C_{ii}C_{jj})^{1/2}. \tag{2}$$

Two sufficient conditions for cost subadditivity are testable with the long-run profit function. The first-sufficient condition is convexity in the cost function and ray subadditivity (Baumol, et al., Sharkey). This condition can be tested with the long-run profit function by examining for convexity the Hessian submatrix of costs with respect to outputs, $[H_{ij}]^{-1}\ \forall\ i, j \in M$. As noted above, increasing multiproduct returns to scale indicate declining ray average costs. A second-sufficient condition for cost subadditivity is transray convexity of the cost function and declining ray average costs (Baumol, et al., 1982; Sharkey, 1982). As before, increasing multiproduct returns to scale indicate declining ray average costs. Because weak cost complementarities among all product pairs are a sufficient condition for transray convexity, failure to establish the result provides evidence against transray convexity. The nature of transray convexity among all product pairs provides additional evidence on overall transray convexity at Y: failure to establish transray convexity among all product pairs indicates that overall transray convexity does not hold (Wang Chiang, 1981).

Market equilibrium

MacDonald and Slivinski (1985, 1987) show that multiproduct market equilibrium can take one of three forms: (1) pure specialization, in which no diversified or multiproduct firms operate; (2) pure diversification, in which no single-product firms operate; or (3) mixed equilibrium involving both diversified and specialized firms. The form of equilibrium depends upon the existence of an advantage in variable or fixed costs for either specialized or diversified firms.

INDUSTRY BACKGROUND

The multispecies New England otter trawl industry exploits some of the world's most valuable fishing grounds. The most important species harvested (in order of value) include cod, yellowtail and other flounders, haddock, redfish, and pollock. Firms are typically quite diversified in product mix although usually oriented toward particular product combinations. The aggregate demand for fresh and frozen fish is much larger than the quantity harvested by the fleet, and excess demand is satisfied by a substantial volume of imports. The harvested fish are marketed fresh in a variety of ways at the ex-vessel level. The ports of New Bedford and Boston contain important spot or auction markets, where fishermen sell their catches to the highest bidder. An important co-operative exists in Point Judith to which members are generally obliged to sell their harvests. In other ports the catch is sold directly to fish processors and brokers or by prior arrangement between individual vessels and fish processors (Wilson, 1980). Product prices vary by vessel.

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[6] Formally, a cost function C exhibits transray convexity along the hyperplane $\Sigma\, a_i Y_i = L$, $\forall\ a_i > 0$, if for any vector of products Y' and Y'' on L, $C(bY' + (1 - b)Y'') \leqq C(Y') + (1 - b)C(Y'')$, $0 < b < 1$. Thus the costs of producing a weighted sum of outputs jointly along any given transray cross section will be less than the weighted costs of individual production.

Area can affect the production technology and cost structure through port effects on prices and institutional practices. Spatial variation in resource abundance is also important; cod is ubiquitously distributed, the flatfish are generally in central and southern waters, pollock and redfish tend to be in northern waters, and the underutilized miscellaneous species are generally in the warmer southern waters. Because of the inherent mobility of boats, all vessels can readily move up and down the coast but seldom to a great distance on any given trip. Boats can also primarily harvest in either offshore or inshore waters; the composition of fish stocks differs by these areas. Inshore vessels are more constrained by inclement weather and rough seas, often cannot harvest from offshore grounds, and make more frequent trips of less duration. Most fish species are harvested throughout the year. Seasonality is most important by virtue of its limiting smaller and inshore vessels in periods of rough weather and seas.

Few fishing firms are horizontally integrated to include two or more vessels, and individual owners operate most vessels. Vertical integration between shore-side processors and boats remains limited to the O'Hara Corporation of Rockland, Maine; instead, the trend over the past two decades is toward divestiture. The industry does not contain any vessels integrating the harvesting and processing functions, nor are mother ships employed.

EMPIRICAL IMPLEMENTATION

Translog profit function

Fishing vessels harvest multiple species with the levels and composition of catch as decision variables of the firms. Fuel, labour, and capital (in the form of the vessel, gear, and equipment) are organized to produce these multiple products. Fishing firms may be regarded as multiproduct firms producing a vector of endogenous outputs from a vector of endogenous inputs. The endogenous outputs and inputs suggest that a profit rather than cost or revenue function is the appropriate dual representation of the firm's production technology. In particular, the multiproduct profit function framework allows endogenous products without the econometric problems of simultaneous equations or the assumption of homothetic separability otherwise required for cost functions.

The translog multiproduct restricted profit function used for the empirical analysis is specified as a second-order Taylor's series approximation around the unit vector by scaling all variables by their arithmetic mean:

$$\begin{aligned}\ln \mathrm{HR} = {} & A_0 + A_T T + A_{\mathrm{IN}}\mathrm{IN} + \Sigma_r A_r R_r + \Sigma_i A_i \ln P_i + A_K \ln K \\ & + \Sigma\Sigma_{ij} A_{ij} \ln P_i \ln P_j + A_{KK} \ln K \ln K + \Sigma_i A_{iT} \ln P_i T \\ & + \Sigma_i A_{i\mathrm{IN}} \ln P_i \mathrm{IN} + \Sigma\Sigma_{ir} A_{ir} \ln P_i R_r + \Sigma_i A_{iK} \ln P_i \ln K. \qquad (3)\end{aligned}$$

Variables are defined as above and in further discussion below. The revenue and cost share equations by Hotelling's Lemma are

$$\begin{aligned}\partial \ln \mathrm{HR}/\partial \ln P_i = P_i Y_i/\mathrm{HR} = U_i = {} & A_i + A_{iT}T + A_{i\mathrm{IN}}\mathrm{IN} + \Sigma_r A_{ir} R_r \\ & + \Sigma_j A_{ij} \ln P_j + A_{iK} \ln K, \qquad \forall\, i \in M, N, \qquad (4)\end{aligned}$$

which are negative for inputs and positive for outputs. Without loss of generality, symmetry requires $A_{ij} = A_{ji}$, $i \neq j$, $i, j \in M, N$, and linear homogeneity in the variable prices requires: $\Sigma_i A_i = 1$, $\Sigma\Sigma_{ij} A_{ij} = \Sigma_i A_{ij} = \Sigma_j A_{ij} = \Sigma_i A_{iK} = \Sigma_i A_{iT} = \Sigma_i A_{i\mathrm{IN}} = \Sigma_i A_{ir} = 0$. These restrictions are directly imposed.

Resource abundance is specified as a technological constraint, since it is beyond the control of any individual firm but nevertheless affects the production environment within which the firm operates. Changes in resource abundance may then be viewed as shifts in the production technology that relates the generation of outputs from inputs (McFadden, 1978; Gordon, 1954). These changes are indexed by the 1981 dummy variable T, where the intercept is 1980.

Three dummy variables R_r designating vessels' home ports are specified to capture area affects: New Bedford, Rhode Island, and Maine. The intercept includes Gloucester, Boston, and other Massachussetts ports. A dummy variable IN for vessels averaging trips of less than two days duration indexes inshore vessels.

The restricted profit function (3) and revenue and cost share equations (4) have additive disturbances, owing to errors in optimization and the stochastic nature of fishing. The large number of harvesters and processors and the presence of auction markets assure exogenous product prices. Factor prices are exogenous because inputs are exchanged regionally and even nationally. Since the share equations sum to unity, the energy consumption equation is dropped and its parameters are identified through the linear homogeneity and symmetry restrictions. The system of equations (3)–(4) is estimated by maximum likelihood using TSP 4.0D, and the results are invariant to choice of deleted equation.

The expressions for long-run pairwise weak-cost complementarity and product-specific incremental marginal costs with the translog multiproduct profit function are derived in the same manner as the long-run factor demand elasticities presented in Brown and Christensen (1981) and Kulatilaka (1985), so that only their final forms are presented. Equation (1) with the translog form becomes

$$H_{ij} = (\mathrm{HR}/P_iP_j)[(A_{ij} + U_iU_j) - (A_{iK} + U_iU_K)(A_{jK} + U_jU_K)/(A_{KK} + U_K^2 - U_K)]. \quad (5)$$

Equation (6) below with the translog form for an individual product provides the basis for the non-statistical test of product-specific incremental marginal costs.

$$H_{ii} = [(\mathrm{HR}/P_i^2)(A_{ii} + U_i^2 - U_i) - (A_{iK} + U_iU_K)^2/(A_{KK} + U_K^2 - U_K)]. \quad (6)$$

The measure for multiproduct returns to scale with the long-run translog profit function is

$$({}_i\Sigma_N\, U_i + U_K)/({}_j\Sigma_M\, U_j). \quad (7)$$

Since measurement is taken along the expansion path, this is also a measure of long-run overall size economies.

The data

The balanced panel data set consists of annual observations for two years, 1980 and 1981, on forty-two full-time otter trawlers with home ports in all of the major and most minor New England ports. Three outputs are specified in the profit function (3) and share equations (4): roundfish (cod and haddock), flatfish (yellowtail and other flounders), and a residual, all others (pollock, redfish, miscellaneous species).[7] Two variable inputs are specified: labour (including captain) and energy (fuel and oil) consumption. The quasi-fixed input, capital, is represented by the vessel's gross registered tons (GRT). The return to labour is measured by its opportunity cost. The opportunity cost of labour per crew member is a Divisia index of the mean annual opportunity incomes of the crew (total manufacturing), the mechanic (maintenance mechanic, machinery), and captain (20 per cent higher than an ordinary seaman's), and varies by vessel and port. These data are from the U.S. Bureau of Labor Statistics and comparable state agencies. Most vessel acquisition prices are obtained from receipts and are measured without error; the remainder are from federal tax returns. Fuel prices are cash prices for number two diesel

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[7] The roundfish and flatfish species assemblages are Divisia indices, while the all others assemblage linearly aggregates over fifty different species. There are fifty-eight parameters to be estimated in the profit function and eighty-four observations. The limited number of observations precludes introducing fixed effects into the profit function, which would require estimation of forty-one additional parameters.

TABLE 1

Summary statistics of data

Variable	Mean	Minimum	Maximum
Price of roundfish	0.1961	0.1502	0.2630
Price of flatfish	0.2575	0.1694	0.3808
Price of all others	0.1494	0.0104	1.2841
Price of fuel	0.5812	0.5143	0.6611
Opportunity cost of labour per person	7801.1	6975.3	9715.7
Capital services price	42949	6100	155908
Pounds of roundfish	439623	2596	1268439
Pounds of flatfish	284993	26148	1091562
Pounds of all others	883201	4763	17925792
Crew size	5.29	2	10
Gross registered tons	120	22	314
Maine engine horsepower	514	225	1400
Days absent from port	167	85	249
Number of trips per year	57	14	257
Profit shares offshore vessels			
Roundfish	0.4033	0.0087	1.636
Flatfish	0.5163	0.0243	1.526
All others	0.7379	0.0283	1.706
Labour	0.3795	0.1043	1.508
Fuel	0.2780	0.0785	0.861
Capital	0.2819	0.0742	0.834
Profit shares inshore vessels			
Roundfish	0.8346	0.1310	1.845
Flatfish	0.5732	0.1159	1.075
All others	0.1983	0.0051	0.689
Labour	0.3267	0.1379	0.754
Fuel	0.2793	0.1058	0.937
Capital	0.2834	0.1464	0.750

NOTES
All values are in $1972 after deflation by GNP implicit price index.
All values are per vessel per year.
Data sources are described in text.

fuel from marine fuel docks. Fuel cost data are from federal income tax returns. Vessel-specific revenue and landings data and vessel and crew size are from the National Marine Fisheries Service's Weighout File. All values are deflated by the GNP implicit price index. Most data are confidential and proprietary. Table 1 provides a summary of the data set.

EMPIRICAL RESULTS

The estimated parameters of the translog multiproduct restricted profit function are reported in table 2.[8] The system's R^2 is 0.99, which is very close to

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[8] Each column in table 2 (except that labelled profit function) represents the parameter estimates corresponding to the ith revenue or input share equation. By assumption, the corre-

1, thereby indicating that the goodness-of-fit of the estimation is very good. The fitted share equations are consistent with monotonicity for all sample values. The restricted profit function is not convex in prices at the point of approximation, although this is not a statistical test.[9] The profit function is concave in the quasi-fixed factor.

Optimal capital stock

A numerical solution is required to solve for the optimal capital stock, $K^* = K^*(P, P_K)$, since a closed-form analytical solution is not possible with the translog form. Because the data are normalized to unity at the arithmetic sample mean, the parameter estimates in table 2 are employed to solve for the percentage deviation from the optimal long-run equilibrium stock of capital. Separate mean capital services prices per gross registered ton are used for inshore and offshore vessels at the point of approximation.

The divergence between estimated K^* and the observed K may simply reflect sampling error in the estimated optimal stock of capital, which can be tested under the null hypothesis: $K^* = K$. If the null hypothesis is not rejected, then the multiproduct cost structure can be evaluated at the observed level of K; otherwise the estimated K^* is employed. Following Kulatilaka, the delta method is used to derive a first-order Taylor's series approximation for the variance of K^*. A t-test is then constructed for the difference between the ratio K^*/K and unity: $t = [(K^*/K) - 1]/[V(K^*)]^{1/2}$, which is t-distributed, where $V(K^*) = K_A{}^*(A)K_A{}^{*\prime}$, A is the vector of estimated parameters and thus is a random variable, $K_A{}^*$ is a vector of partial derivatives of K^* with respect to A, and $K_A{}^* = -(\mathrm{HR}_{KK})^{-1}\mathrm{HR}_{KA}$ evaluated at K^*. Because the use of fitted profit shares in calculating $V(K^*)$ may not provide a normally distributed test statistic with the translog form (Anderson and Thursby 1986), the test statistic is evaluated at the point of approximation using both fitted and mean actual profit shares for 1980.

The ratio of optimal GRT to observed mean GRT for offshore vessels in 1980 is 0.902 (= 106.23 GRT*/117.81 GRT) and for inshore vessels is 0.655 (= 81.92

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sponding parameter estimates of the profit and share equations are equal. Thus the parameter estimates corresponding to equations (3) and (4) are A_i for the intercept, A_{ii} for the own price, A_{ij} for cross-price interaction terms, and A_{iK} for the interaction between the own price and capital. The profit equation column reports parameter estimates unique to the profit equation itself, so that the intercept term refers to A_0 in equation (3), A_T refers to the 1981 intercept term, A_{IN} refers to the inshore dummy variable, R_r refers to the three area dummy variables, A_K refers to the first-order capital variable, and A_{KK} refers to the squared capital variable.

[9] The generalized R^2 is computed as $1 - \exp(2(1_0 - L_1)/N)$, where $L_0(L_1)$ is the sample maximum of log-likelihood when all slope coefficients are zero (unconstrained) and N is sample size (Baxter and Cragg, 1970). A test of convexity cannot be interpreted as strictly a test of profit maximization, because convexity can be violated for a number of other reasons. For example, Wales (1977) shows that the estimates of a flexible functional form may violate convexity even if the data come from a perfectly well-behaved technology. Linear aggregation of over fifty species into the all others assemblage can also cause the apparent failure of convexity.

TABLE 2

Parameter estimates of translog restricted profit function

Exogeneous variables	Product shares			Factor shares		Profit function
	Roundfish	Flatfish	All others	Labour	Fuel[a]	
Intercept	0.875 (0.084)	0.262 (0.070)	0.490 (0.085)	−0.325 (0.061)	−0.303 (0.047)	0.086 (0.142)
1981 dummy	−0.052 (0.070)	0.101 (0.060)	0.092 (0.074)	−0.122 (0.064)	−0.020 (0.042)	−0.142 (0.132)
Inshore	0.066 (0.096)	0.006 (0.078)	−0.251 (0.108)	0.157 (0.084)	0.023 (0.056)	0.191 (0.178)
New Bedford dummy	−0.197 (0.104)	0.456 (0.085)	−0.281 (0.120)	−0.034 (0.093)	0.056 (0.062)	−0.072 (0.197)
Rhode Island dummy	−0.616 (0.106)	0.088 (0.085)	0.212 (0.105)	0.085 (0.951)	0.231 (0.938)	0.303 (0.188)
Maine dummy	−0.510 (0.106)	0.157 (0.080)	0.319 (0.098)	0.105 (0.940)	−0.070 (0.939)	−0.049 (0.165)
Roundfish price	−0.400 (0.255)	0.175 (0.164)	−0.153 (0.055)	0.261 (0.149)	0.117 (0.101)	
Flatfish price		−0.381 (0.167)	−0.144 (0.044)	0.334 (0.113)	0.016 (0.071)	
All others price			−0.060 (0.038)	0.215 (0.036)	0.142 (0.022)	
Opportunity cost of labour				−0.811 (0.179)	−0.001 (0.208)	
Fuel price					−0.276 (0.362)	
Capital	0.292 (0.068)	−0.384 (0.056)	0.229 (0.072)	−0.008 (0.060)	−0.130 (0.039)	0.664 (0.140)
Capital squared						0.114 (0.072)

a Parameter estimates are derived from the constraints implied by linear homogeneity in prices and symmetry.

NOTE: Linearized standard errors are in parentheses.

GRT*/125.00 GRT). The estimated *t* for offshore vessels with actual (fitted) shares is −0.04 (−0.02) and for inshore vessels is −0.16 (−0.15), implying no statistically significant difference between optimal and observed capital stocks for either sector at conventional levels of significance. The test result may reflect a robust level of optimal long-run capital stock in an industry in which fishermen make long-run investment decisions with expectations of important cyclical and stochastic fluctuations in resource abundance over both time and space. Moreover, since a vessel of a certain size and design is required to fish in the stormy north-west Atlantic and to reach the fishing grounds, optimal capital stock is likely to be quite robust.

TABLE 3

Multiproduct Cost Structure

	Weak cost complementarity			Incremental marginal costs
	Roundfish	Flatfish	All others	
Inshore				
Roundfish		−0.771	0.301	0.138
Flatfish			−1.235	−5.260
All others				0.883
Offshore				
Roundfish		−0.789	0.213	0.155
Flatfish			−0.927	−5.780
All others				0.399

NOTES

Evaluated at arithmetic sample mean for all Massachusetts ports in 1980 except New Bedford.
Evaluated using fitted shares calculated with optimal capital.
Weak cost complementarity values calculated using equation (5).
Incremental marginal cost values calculated using equation (6).

Multiproduct cost structure

Table 3 presents the estimated 1980 structure of long-run multiproduct costs evaluated at the optimum (equals observed) capital stock for both inshore and offshore vessels. The results are calculated using fitted shares evaluated at the point of normalization and optimal (here equals observed) capital stock. The empirical results calculated using 1980 arithmetic mean values of actual profit shares provide the same qualitative results. Table 1 provides these actual shares.

The results for long-run pairwise cost complementarities indicate that product-specific economies of scope exist between flatfish and the two other products, roundfish and all others, for both inshore and offshore vessels. Flatfish are a pivotal species because cost savings accrue to vessels harvesting flatfish with roundfish and all others. The most important factor contributing to scope economies may be the spatial distribution of different species assemblages among different fishing grounds and latitudes along with the inherent mobility of vessels. The variations in species composition of the resource by latitude and distance from shore tend to impose both upper and lower limits to the extent of scope economies. Seasonality is of minimal importance because important species groups are harvested throughout the year. Fishing skill and experience also contribute. The usual contributors toward economies of scope in multiproduct industries, such as risk minimization and the quasi-public nature of capital, may also be important (cf. Bailey and Friedlaender, 1982; Baumol, et al., 1982; Sharkey, 1982). The similarity of factor proportions for different products may also contribute (MacDonald and Slivinski, 1985).

The incremental marginal costs results for both inshore and offshore vessels suggest the presence of declining product-specific marginal and average incremental cost curves and increasing product-specific returns to scale for flatfish but decreasing product-specific returns to scale for roundfish and all others. Declining flatfish stocks that are placed under excessive harvesting pressure can cause excess flatfish harvesting capacity, and therefore the declining product-specific cost curves. None the less, even though product-specific returns to scale for flatfish are increasing, specialized flatfish vessels are unlikely because economies of scope are realized by jointly harvesting flatfish with other species.

The 1980 estimate of long-run multiproduct returns to scale using fitted shares is 0.79 for offshore vessels and 0.77 for inshore vessels, indicating decreasing overall returns to scale for both sectors. Cost or profit advantages do not accrue from increasing production in fixed output proportions holding prices and resource abundance constant. As the scale of production expands for a given level and mix of resource abundance, vessels fish in more marginal grounds, further deplete the resource stocks in existing areas, fish in more adverse weather, and so forth. The decreasing product-specific returns to scale and limits to economies of scope contribute toward the decreasing ray returns.

The two sufficient conditions for cost subadditivity are not satisfied by the empirical results. The evidence of decreasing overall returns to scale indicates that ray subadditivity is unlikely. Cross-sectional economies are also limited, since only limited pairwise weak-cost complementarities and no pairwise transray convexities are found. Moreover, evaluation of the Hessian submatrix of outputs pertaining to the cost function indicates the absence of uniformly positive-definite diagonal elements and principal minors which are not all positive semi-definite. The cost surface is not convex with respect to outputs. Some form of fishermen's monopoly does not provide the most efficient method by which to organize production.[10]

Multiproduct industry structure

The multiproduct cost structure indicates that New England fishing firms under open-access resource conditions face definite limits to the private cost savings they could enjoy from expanding the scale and narrowing the scope of their production. Vessel orientation remains coastal, and does not emulate the large vessels of the foreign distant-water fleets. Large vessels of that magnitude require enormous levels of resource abundance, such as that realized by harvesting in a world scale. This factor and the high search costs of locating fish contribute toward the constant movement and pulse fishing of distant-water fleets.[11] The relatively high opportunity cost of labour and the relatively low opportunity cost of animal protein in the United States further increase the costs of operating large distant-water fleet vessels by New England fishermen. In contrast, distant-water fleets composed of large catcher-processors tend to be successfully operated by nations with a sufficiently advanced industrial base and higher opportunity costs of protein production from agriculture and / or lower opportunity costs of labour, such as the socialist bloc nations, the countries of north-east Asia, and several western European nations.

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[10] Monopoly organization which optimizes the amount of social fishing effort over time might be socially efficient by mitigating market failure from congestion and stock externalities. The procedure developed in this study does not consider any extant external costs and benefits, and is static in the population dynamics.

Specialized firms are limited, because both the fixed and variable costs should be lower for diversified firms than for specialized firms. The increasing product-specific returns to scale occurs with the same species assemblage, flatfish, which realizes economies of scope with both the other outputs. Although under current open-access resource conditions flatfish revenues alone are insufficient to cover the incremental costs of its production, sufficient cost savings are generated because of the scope economies to insure continued flatfish harvesting. That is, the economies of scope sufficiently outweigh product-specific scale effects for flatfish. Variable costs of diversified firms are therefore less than those that would occur with specialized firms.

The structure of fixed costs further contributes to the absence of specialized firms. The absence of cost subadditivity, presence of decreasing ray returns to scale, and capital at its optimum level suggest definite limits to the magnitude of fixed costs arising from the production technology. That is, these fixed costs are relatively small, particularly in comparison to the overall level of industry output, which MacDonald and Slivinski (1985) indicate favours a diversified equilibrium.

Costs arising from the organizational technology also limit firm specialization. Intangible assets such as technological knowhow, management, and information can be divided into a pure public input of overall knowledge of fishing and seamanship and into product-specific knowledge about different species and grounds. Because up to some point product-specific knowledge can be acquired at minimal additional costs through the general process of fishing, the incremental fixed knowhow and informational costs of producing additional species are comparatively small, which allows all fixed costs to be spread among more outputs. This spreading of fixed costs and sharing of intangible assets among additional outputs, in turn, generates scope economies (Baumol, et al., 1982; Gormon, 1985; Teece, 1980, 1982), and further favours diversified over specialized firms.

Prohibitive transactions and information costs are perhaps the most limiting constraint to firm amalgamation of these multiproduct firms. Coase (1937) argues that activities are collected in a firm when the transactions costs incurred using the price mechanism of a market exceed the costs of organizing the activities through direct managerial controls. The firm will expand until the marginal value of an additional transaction internal to the firm equals the cost at the margin of increasing the size of the firm. These costs, or diseconomies of scale to firm size, are in turn related to the fixed supply of entrepreneurial input and the high costs of obtaining information as well as organizational and strategic impediments to its market transfer (Williamson, 1979; Teece, 1980, 1982; Sharkey, 1982).

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[11] Pulse fishing refers to the practice of heavily exploiting a given area and then moving on to a new area.

Fishing is particularly sensitive to entrepreneurial and managerial ability, especially at the vessel level, because it is a semi-systematic, spatially dispersed hunting process. Information on location and availability of fish is therefore important. Since the plant dimension is the vessel, which is an indivisible and lumpy asset, and the vessel is very mobile and spatially dispersed from other vessels, transferring information from one vessel to another is costly and difficult. Moreover, attracting and retaining competent skippers with high skill levels in multivessel firms is difficult. Because vessel acquisition prices are sufficiently small, a skilled captain can easily aspire to vessel ownership, and capable skippers have high opportunity costs to vessel operatorship without ownership.[12]

Successful multivessel firms instead tend to be owned and operated only under circumstances substantially reducing transactions and information costs between vessels. The most common occurrences are ownership by an extended family employing family members as skippers, which removes transactions costs from market valuation, and ownership by very experienced fishermen intimately involved in operating their vessels. The latter can also attract competent crews and skippers and captain vessels when necessary. Thus, other than under exceptional circumstances, organizational diseconomies limit horizontal integration of these multiproduct but single-vessel firms.

The cost structure also inhibits vertical integration of the processing and harvesting sectors. Following Williamson, the criterion for organizing commercial transactions is assumed to be cost minimization. Vertical integration entails removing transactions from the market and organizing them internally within the firm. Vertical integration of harvesting and processing in this industry necessarily implies horizontal integration of vessels or a large expansion in the scale of production. Costs are instead lowered by procuring fish supplies through the market rather than organizing production internally to the firm, since the cost structure typically precludes multivessel firms or expanding the scale of production. Stable and adequate supplies are also available to processors from the large number of individual vessels or fish brokers, thereby reinforcing the more efficient cost structure attained by separating the ownership of harvesting and processing with a more limited scale of production. Backward integration into production by processors is instead more likely if resources are scarce and supplies uncertain. Production risks are also retained by producers, particularly the crew, because of the share of labour remuneration system. The relationship between processors and harvestors remains predominantly a bilateral governance structure, in which the autonomy of the parties is maintained (Wilson, 1980).

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[12] Although the economic returns to solely vessel ownership may be limited (unless for tax shelter purposes), ownership in conjunction with the captain's share, any efficiency rents due to skill, and non-pecuniary returns from this way of life then lead to an attractive overall return.

Monopoly reasons for merger also do not exist, nor are there advantages to obtaining vessels cheaper through merger than through purchase. Economies of networking and materials procurement are also not factors. Some capital-raising or other similar pecuniary economies probably exist, but they are not dominant factors.

The structure of transactions costs also favours diversified (but single-vessel) firms. Technology and fishing skill transfer opportunities among different species groups are recurrent rather than occasional (because of the indivisible and spatially dispersed vessel as a quasi-public input), and the application specialized rather than non-specialized. Intrafirm production of multiple products therefore lowers transactions costs more than two specialized firms contracting among themselves in order to enjoy economies of joint production (Teece 1980, 1982).

CONCLUDING REMARKS

The structure of long-run multiproduct costs indicates that industry structure is likely to remain atomistic, displaying minimal vertical and horizontal integration of firms. Individual owner-operatorship of single-vessel, multiproduct firms remains the norm. Evidence is not provided for private efficiency gains from industry concentration or centralization through expanding the scale or scope of production, horizontal integration, or a fishermen's monopoly. Family ownership and operation remain feasible, and the possibility exists of purchasing smaller boats and moving up in scale as experience and savings are accumulated. Any open-access multiproduct equilibrium that might exist is likely to be diversified, because both variable and fixed costs should be lower for diversified firms than for specialized firms.

The long-run multiproduct profit function offers a convenient framework to analyse the technological and cost determinants of multiproduct industry structure and the likely form of equilibrium. The levels and mixes of outputs are decision variables to firms, the long-run equilibrium levels of any quasi-fixed factors are endogenously determined, and a ready distinction is made between variable and fixed costs.

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EUPHAUSIID PREDATION ON LARVAL ANCHOVY AT TWO CONTRASTING SITES OFF CALIFORNIA DETERMINED WITH AN ELISPOT IMMUNOASSAY

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INTRODUCTION

Understanding the processes affecting recruitment is a fundamental objective in fishery research. Starvation and predation are believed to be the major factors influencing survival of young fish (Hunter, 1984), and mortality due to these two factors must be quantified to understand how they control recruitment of young fish to a fish stock.

Evidence supporting the occurrence of starving larval fish in the ocean was mainly circumstantial (May, 1974; Jones and Hall, 1974; Lasker, 1975) until recently, when the presence of starving ocean-caught larval northern anchovy, *Engraulis mordax*, was documented using histological criteria (O`Connell, 1980). Subsequently, using similar criteria, Theilacker (1986) quantified starvation-induced mortality for ocean-caught larval jack mackerel, *Trachurus symmetricus*, and showed that starvation was a significant source of mortality for first-feeding fish.

Limited information is available on predation of larval fishes. Field evidence of predation by crustaceans has been mainly circumstantial (Westernhagen and Rosenthal, 1976; Alvariño, 1980; Frank and Leggett, 1982; Bailey and Yen, 1983; Brewer *et al.*, 1984), yet many crustaceans eat larval fish under laboratory conditions (reviewed by Hunter, 1984). Little field information exists for carnivorous Crustacea because they macerate their prey and prey remains cannot be visually identified. However, predation on larval fishes by pelagic cnidarians and ctenophores, gelatinous predators, was documented in the field and, in some cases, quantified (Moller, 1984; Purcell, 1981; 1984). Furthermore several field studies have demonstrated that planktivorous fishes also consume fish eggs and larvae (reviewed by Hunter, 1984).

Off California, the euphausiid crustacean *Euphausia pacifica* co-occurs temporally and spatially with northern anchovy larvae. In February and March, during northern anchovy spawning season, field collections containing 5000 adult euphausiids per m^3 are common (Brinton and Wyllie, 1976). In the laboratory, adult *E. pacifica* can consume up to 25 larvae per day (Theilacker and Lasker, 1974). If this feeding rate occurs in the ocean, euphausiids could be an important predator of larval anchovy.

These results are of a preliminary field study conducted to test the feasibility of using a newly developed immunoassay to assess predation on larval anchovy by euphausiids. *E. pacifica was sampled* from two contrasting sites off California. The inshore site was within an area of intense anchovy spawning, and the offshore site was outside of the main spawning area. An ELISPOT immunoassay was used to detect the presence of northern anchovy yolk protein in the euphausiids' stomachs (Theilacker *et al.*, 1986). Evidence obtained shows that euphausiids eat anchovy eggs and/or larvae; quantification of the euphausiid consumption rate in the field; and suggests that the predation by euphausiids may be significant.

This preliminary study proved the feasibility of using the ELISPOT technique for field samples. A more comprehensive spatial and temporal estimation of anchovy egg and larval mortality due to predation by euphausiids will be made next year. The proposed research is discussed.

METHODS

Field Collection

Inshore collections were made in March 1985 at two sites, 8 miles apart, 50 miles off the coast of southern California where anchovy spawning was intense. The offshore collection was made in February 1986, 100 miles off the southern California coast where anchovy spawning was minimal. These collections were made aboard the NOAA Ship David Starr Jordan. Between 2200 and 0200, 5 minute oblique tows were taken to 50 m, the depth where euphausiids and larval northern anchovy co-occur for about 10 h at night (Ahlstrom, 1959; Brinton, 1976). A Bongo frame was used, fitted with a 505 µm mesh net and plastic cod ends. After carefully diluting the live euphausiids into several buckets containing 14°C surface seawater, swimming animals were selected, blotted and placed individually into

1 ml Eppendorf tubes set in crushed ice. The sorting process, from seawater to cooled tube, took about 1 min per animal. Groups of animals were frozen every 10 min in liquid nitrogen and stored at -80° C.

In addition to the euphausiid collections, quantitative, oblique plankton tows were taken with a 505 µm mesh Bongo to a depth of 200 m at the inshore and offshore sites. Abundances of anchovy eggs, yolk-sac larvae, and adult (12-22 mm) and juvenile (6 - 11 mm) euphausiids were estimated from these samples.

Laboratory immunoassay

To test for the presence of anchovy yolk protein (which cannot be visually detected or identified) in the stomachs of field-collected *E. pacifica*, an immunoassay (Enzyme-Linked Immunospot; ELISPOT) was used that detected nannogram quantities of anchovy egg-yolk protein in stomach of laboratory-fed euphausiids. The details of the ELISPOT assay are given by Theilacker *et al.* (1986). The individual, field-collected animals were prepared for the assay by dissecting the stomach, hepatopancreas, and hindgut, teasing the tissues in buffer, and dotting the extract, about 10 µl, onto nitrocellulose paper (0.45 µm pore size). For the ELISPOT procedure, after the antigen (unknown gut contents; potentially, anchovy yolk protein) was immobilized on nitrocellulose, the antigen was then reacted with the primary antibody to anchovy yolk protein which was produced in rabbits. The resulting antigen-antibody complex was treated with a secondary antibody which had been tagged with the enzyme alkaline phosphatase. This secondary antibody was produced in goats by immunizing them with rabbit sera. The complex on the nitrocellulose was visualized with a dye, and positive phosphatase activity produced a blue-black reaction.

Control euphausiids, fed algae in the laboratory for 24-48 h at 14° C to clear their guts of non-algal prey, were dissected and run with each test. A test consisted of one control animal with 6-9 unknowns; as many as 6 tests were run simultaneously with this assay. Dotted gut contents from field animals that developed color visually darker than the gut contents of the control animals were counted as positive. In this application, the immunoassay was used to detect presence or absence of yolk in the predator's stomach. That is, even though the protein quantity is measurable with the assay, the number of larvae eaten cannot be quantified because the absolute amount of yolk contained in an individual egg and yold-sac larva descreases with age.

RESULTS

A total of 114 adult *E. pacifica* were taken at the two inshore collections. The fraction positive at the first site was 43/55 (78%) and at the second site was 47/59 (80%). Offshore, the fraction positive was 5/65 (7%).

At the two inshore sites euphausiid abundance, estimated as the number of individuals under 10 m^2 sea surface, was 192 and 542 adults and 526 and 927 juveniles; offshore, the number of individuals was 3376 adults and 399 juveniles (Table 1).

Estimates of anchovy egg and larval abundance inshore (estimated, as above, for numbers/10 m^2 sea surface and summed over the duration, 6 days, that eggs and larvae are eaten by predatory euphausiids, see Theilacker and Lasker, 1974) were 18207 eggs and 3200 yolk-sac larvae; estimates for the offshore site were 1942 eggs and 240 yolk-sac larvae (Table 1).

To estimate daily consumption by the euphausiid population, additional field and laboratory information was needed. Brinton's (1976) field data on vertical distribution of *E. pacifica* showed that for 10 hours at night 87% of the animals occur in the upper 50 meters of the sea surface, which is the depth distribution for northern anchovy eggs and larvae (Ahlstrom, 1959). Earlier laboratory studies revealed that juvenile *E. pacifica* feed at one third the rate of adults (Theilacker and Lasker, 1974). Thus to calculate total predation by euphausiids the number of juveniles was adjusted by 0.3 (Table 1; footnote 2). The final information needed, euphausiid digestion times at *in situ* temperatures, was taken from the results of a digestion experiment where 12 adult euphausiids that had eaten 1 or 2 anchovy larvae were subsequently fed copepods and algae for 1 to 6 h. More experiments are needed, but preliminary results showed that yolk protein was undetectable in the euphausiid guts after 4 h digestion. For this study, a digestion time of 4 h was assumed to calculate euphausiid feeding rates.

A Poisson distribution was used to calculate the mean number of anchovy eggs and larvae in a euphausiid's stomach because the mean of a Poisson distribution can be easily estimated directly from the frequency of "0" counts, or negative assays ($\mu = -\ln f(0)$). As mentioned earlier, the immunoassay technique determines presence or absence of anchovy yolk protein and does not provide information on how many prey were consumed. Thus the positive assays combine counts of one or more eggs or larvae, and the negative assays identify the euphausiids that had not eaten anchovies in the last 4 h, the assumed digestion time. Using the Poisson distribution, the mean number of eggs or larvae eaten per 4 h is equal to *-ln* of the frequency of negative assays. Because the euphausiids and anchovy co-occur for 10 h per day, the number of anchovy eggs and larvae eaten per day is 2.5 μ (Table 1; footnote 2). This relation was used to estimate the impact of euphausiid predation on the anchovy population at the two contrasting sites given the above laboratory and field information (Table 1).

Table 1.

	ESTIMATED ABUNDANCE/10m^2		PREDATION BY EUPHAUSIIDS		
	ANCHOVY (eggs/larvae)	EUPHAUSIIDS (juv./adults)	ELISPOT (fraction +)	EST. FEEDING RATE/10h (indiv./pop.)	% ANCHOVY POPULATION EATEN
Inshore$_1$	18,207/3200	526/192	43/55	3.8^1/1,156^2	5
Inshore$_2$		927/542	47/59	4.0/2,854	13
Offshore$_1$	1,942/240	399/3,376	5/65	0.2/608	28

[1] Poisson distribution $f(0) = e^{-\mu}$; $\mu = -\ln f(0)$ = mean number eaten/4h

[2] Number eggs or larvae eaten/10h = (number adult euphausiids + 0.3 number juveniles) x 2.5μ x 0.87

The egg and larval (yolk-sac) mortality rates due to euphausiid predation at the inshore sites were 0.05 and 0.13/d, with an average of 0.09 (percent of anchovy eaten; Table 1). At the offshore station, daily anchovy mortality due to euphausiid predation was 0.28. The total instantaneous mortality rate (Z) calculated from the above egg (N_1) and larval (N_2) data for the inshore site was 0.6/d and for the offshore site was 0.7/d ($Z = \ln N_1 - \ln N_2)/(t2-t1)$). Thus the results from this preliminary study show that the difference in mortality between the inshore and offshore sites can be accounted for by differences in rates of euphausiid predation.

DISCUSSION

This preliminary study shows that invertebrate predation rates can be estimated by using the ELISPOT immunoassay together with additional laboratory and field data. Refining recruitment estimates may be possible by combining information on predation mortality together with estimates of total larval fish mortality and starvation-induced mortality.

Efforts to make a comprehensive spatial and temporal evaluation of anchovy mortality due to predation by euphausiids are being planned. Three two-week cruises, beginning in November, 1986, will be conducted to sample the northern anchovy habitat off California before, during and after peak spawning. A net with a larger mesh, 2 mm, will be used to collect the animals. This net allows eggs and larvae to pass through, precluding biases caused by euphausiids feeding in the cod-end (Nicol, 1984). Short, 5 minute tows were used in the preliminary study reported here to decrease the probability of cod-end feeding. In the laboratory, additional euphausiid digestion experiments will be conducted with adult and juvenile animals.

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The Traditional Central California Setnet Fishery

EDWARD UEBER

Introduction

Setnets, curtainlike fishing gear designed to entangle fish or catch them by the gills, have been under study in recent years. In 1984, the California Department of Fish and Game (CDFG) began a study of the central California setnet fishery to determine its scope and the incidence and magnitude of captured birds and mammals. Concurrent with this study was a continuing project conducted by the national Sea Grant Program and the National Marine Fisheries Service to develop methods less controversial than setnet fishing and, where possible, to introduce new gear which would capture the desired fish but not birds and mammals.

Another reason for the study was a desire by industry and the CDFG for an economic assessment of the fishery. The California legislature wanted to learn the number of active setnet fishermen and the importance of setnet revenues to fishermen's total income. Two other areas of legislative interest were fuel consumption and safety conditions aboard setnet vessels.

The foremost objective of this study was to determine the number of active setnet fishermen and to provide an economic and descriptive profile of the setnet fishery. Secondary objectives were to assess the costs of setnet fishing and the ex-vessel revenues attributable to it, and to gather information about vessel fuel use.

The setnet fleet was known to consist of Vietnamese and non-Vietnamese (traditional) fishermen. Due to language difficulties, the author was unable to obtain information from Vietnamese fishermen. This report, therefore, represents only the traditional sector of the central California setnet industry.

ABSTRACT—*In 1984, the central California traditional (non-Vietnamese) setnet fishery was calculated to consist of 266 fishermen fishing from 133 different vessels. These men fished with set gill, trammel, and suspender nets predominantly for halibut, ; rockfish,* Sebastes *spp.; white croaker,* Gengonemus lineatus*; shark (Squaliformes); lingcod,* Ophiodon elongatus*; and sablefish,* Anoplopoma fimbria. *The estimated capital value of the traditional setnet vessels and the setnet gear in 1984 was $11,000,000. Fixed and variable costs (excluding crew wages) were estimated at around $3,500,000, and ex-vessel revenues were about $4,000,000. Results in this report pertain only to the traditional setnet fishery and should not be extrapolated to include either the Vietnamese fishermen or the fishery in which Vietnamese setnetters fish.*

Background

In California, setnets include gill nets and trammel nets. Trammel nets include the traditional three-wall trammel nets ("trammel" nets) and suspender gill nets ("suspender nets"). A gill net is a single-walled net which is hung taut (without slack) (Fig. 1A). Fish are generally caught in such nets by having their gill covers hooked on the netting; this is called gilling.

Trammel nets (Fig. 1B) are three-walled nets with a slack inner wall of small mesh and two outer walls of taut large mesh, one wall on each side of the inner wall. Fish swim through the larger outer mesh, strike the small inner mesh, and push the small mesh through the other outer wall. This loop of small mesh forms a pocket and the fish are trapped (Clark, 1931).

Suspender nets are legally designated as trammel nets in CFG Code 8700 and are identical to gill nets except that lines (suspenders) are attached between floatrope and footrope (Fig. 1C). The suspenders cause the single-wall net to bag or become slack. Suspender nets both gill and entangle fish. Fishermen who use suspender nets claim that they are easier to empty, less expensive, and catch a wider range of species. Trammel net users say that the three-wall net is better for catching halibut, , and that sharks and other fishes do not fall out of the net as easily as from suspender or gill nets.

In 1982, the Pacific Coast Groundfish Plan, developed by the Pacific Fishery Management Council (PFMC) and approved by the Secretary of Commerce as prescribed in the Magnuson Fisheries Conservation and Management Act of 1977, became law. This plan prohibits fishing for groundfish with set trammel or gill nets north of lat. 38½°N (Point Reyes) in the U.S. fishery conservation zone (FCZ). In areas south of lat. 38½°N, Article 5 of the CFG Code, Section 8680 through 8693, is the governing regulation in California ocean waters and the FCZ (PFMC, 1982).

In 1983, 1984, and 1985, Article 5 was changed, and in 1986 new CFG permit regulations were instituted. The new Article 5 does not apply to setnetters fishing in the FCZ[1]. The 1986 permits are nontransferable and obtainable by qualified fishermen only. The new regulations limit the number of permits to 135

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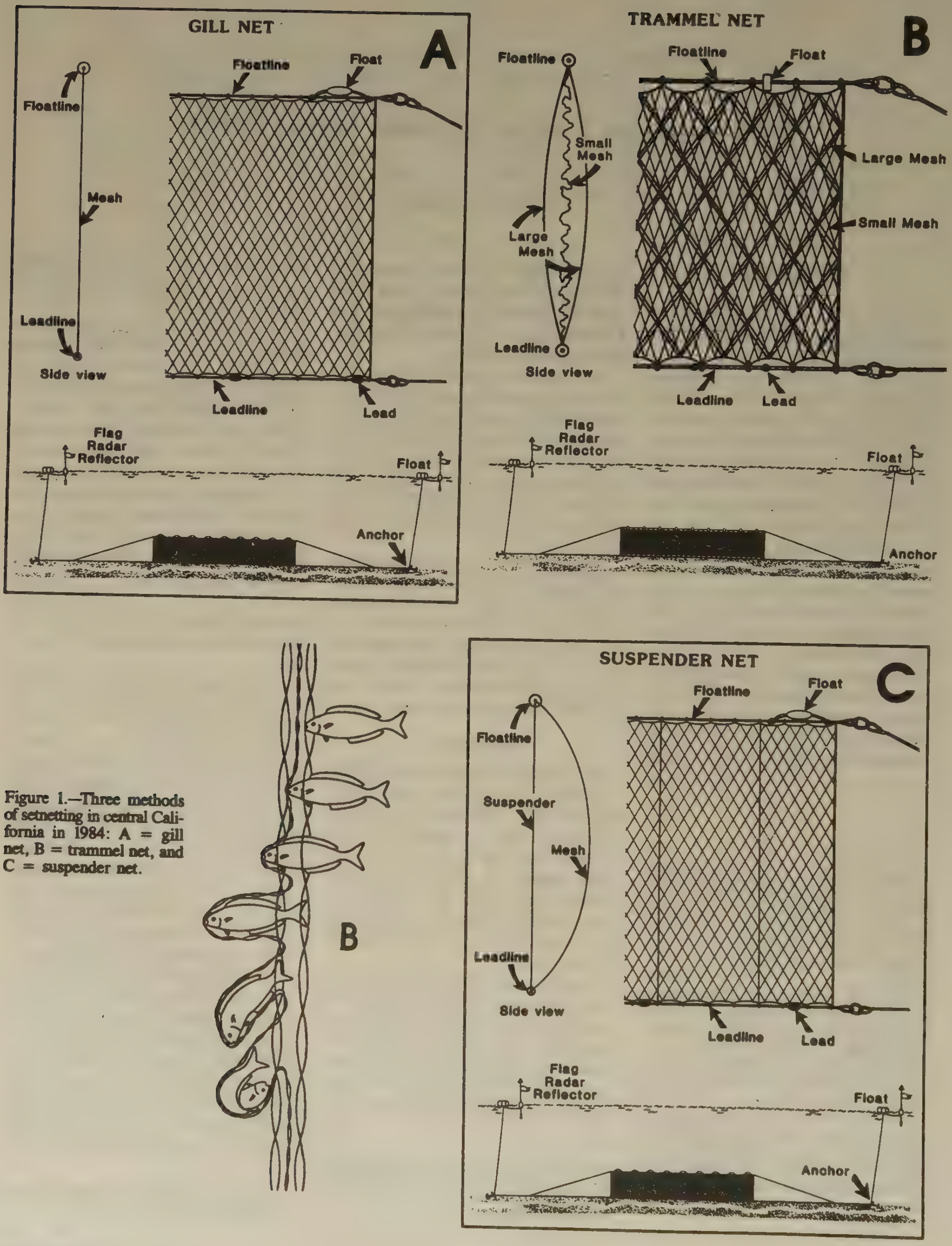
[1] Carper, H. A. 1986. Letter to Joseph C. Greenley, 6 March 1986, Sacramento, Calif.


GILL NET
A
Floatline
Float
Floatline
Mesh
Leadline
Side view
Leadline
Lead
Flag
Radar
Reflector
Float
Anchor
TRAMMEL NET
B
Floatline
Float
Floatline
Small
Mesh
Large
Mesh
Large Mesh
Small Mesh
Leadline
Side view
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Radar
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SUSPENDER NET
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Reflector
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Anchor

Figure 1.—Three methods of setnetting in central California in 1984: A = gill net, B = trammel net, and C = suspender net.

Retrieving a gillnet in the angel shark fishery. Photo courtesy of Constance Ryan.

in the nearshore trammel-net and suspender net fishery for halibut, , and the gillnet fishery for white croaker, *Genyonemus lineatus*, and nearshore rockfish, *Sebastes* spp. It is hoped that these regulations will diminish setnet interaction with other fishermen, birds, and mammals.

History

Setnets which gill or entangle fish have been used in the Americas for over 7,800 years. Archaeologists believe that the Chinchorro society, one of the oldest in the Americas, depended on setnet fishing for its supply of protein (Allison, 1985). Records of setnet fishing also exist from west coast North American native societies. Native Americans of Washington, Oregon, and Canada constructed setnets from line made of stinging nettle. The use of nettle to make line for fishing nets was also known in early Europe. "In fact the word 'net' is derived from 'nettle' " (Stewart, 1977).

In 1878, Spencer F. Baird, introduced setnets from Europe to Cape Ann, Mass., fishermen (Collins, 1882). These nets proved very effective and their use spread quickly. By 1888, gill and trammel setnets were being used in California and accounted for 76 percent of the value of all fishing apparatus in California excluding the value of the vessels (Collins, 1892).

By 1915, only trammel and gill nets were allowed south of Carmel Point, Calif., as trawl and paranzella nets were banned (Scofield, 1915). Set trammel and gill nets and drift gill nets were used in southern California to catch white seabass, *Atractoscion nobilis*; flatfishes, Pleuronectiformes; rockfishes, *Sebastes* spp.; Pacific barracuda, *Sphyraena argentea*; and crabs. White seabass was the most important species taken by setnets before 1930 (Whitehead, 1930), but halibut and rockfishes were also targeted.

The striking feature of all the set and drift nets used through the centuries by disparate peoples is their similarity. Setnets employed by native fishermen in 6000 B.C. were designed and fished exactly as the nets used today in central California. The only difference is the material used in net construction. Lines are no longer made of crushed nettle fiber, but synthetic nylon fiber. Floats of wood, reed, cork, or glass have been replaced by plastic. Anchors of stone have become the exception to the more common steel anchors, and footropes are weighted with lead, not rocks, waterlogged sticks, or ceramic clay.

Although materials have changed, setnets remain devices which gill (gill nets) or entangle fish (trammel nets). Set gill nets used in Calfiornia in 1888 had from 2- to 8-inch mesh; the set gill nets in 1986 had from 2⅛-to 9-inch mesh. Trammel nets in 1888 generally had an inner wall of 8-inch mesh; today 8-inch mesh is still the most frequently used.

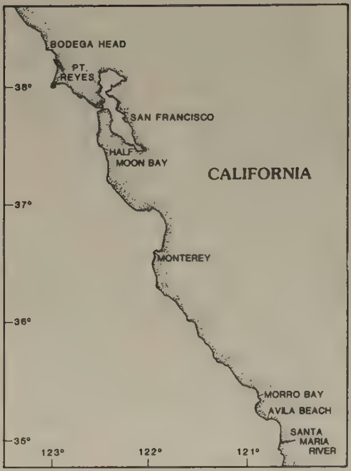
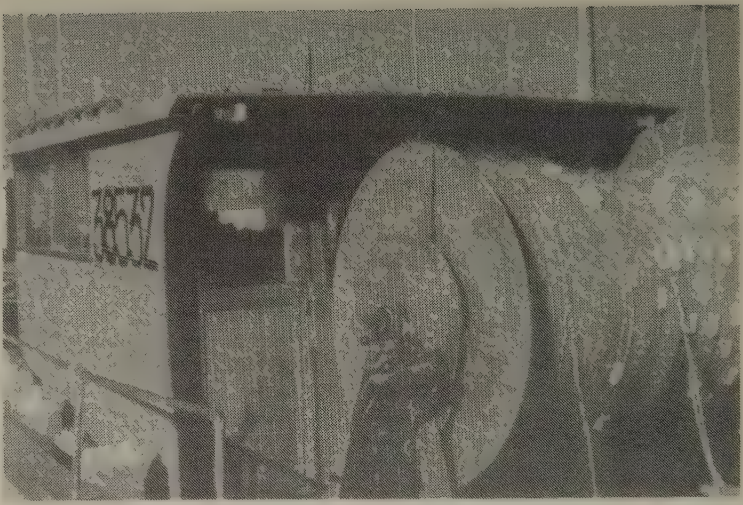


Figure 2.—The study area.



Gillnet on reel, Berkeley, Calif., 1984. Photograph by the author.

There has been a change in California in the public's perception of the deployment, quantity, location, and species which are exploited with set gill and trammel nets. Although fishermen have been using trammel nets to catch halibut and sharks continually since the 1880's, gillnetting of white croaker, rockfishes, and lingcod, *Ophiodon elongatus*, has mostly occurred since 1980. Much of this increase has been by ex-salmon trollers using trammel nets (Anonymous, 1986) and Vietnamese fishermen using gill nets. This expansion has caused public concern because of the incidental catches of marine birds and mammals reported in the media.

Methods

A list of all set gillnet permits was obtained from CDFG offices in Monterey and Menlo Park. These two offices issued over 95 percent of the permits to fishermen who fished from Point Sal (10 miles west of Santa Maria) to Point Reyes (30 miles west-northwest of San Francisco) (Fig. 2). In 1984, 586 setnet permits for fishermen were issued from Monterey and Menlo Park. From these, 120 permits were randomly selected and classified by surname as belonging to either the Vietnamese (40 permits) or traditional (80 permits) component of the fishery. Attempts to interview Vietnamese fishermen were unsuccessful because of language difficulties; therefore, survey results pertain only to the traditional component of the fishery and should not be used to generalize for the entire fishery.

Phone numbers, addresses, and other information, such as vessel locations or fishing companies, were gathered for traditional fishermen from the CDFG, processors, harbor masters, and fishermen's associations. Attempts were made to contact fishermen by phone or in person at their home port or buyer.

Vessel values were obtained from the vessel captains. Some captains felt their current wooden vessels could be replaced more cheaply with new steel vessels. When a captain stated the above, the lesser cost of a steel vessel was used to represent replacement value. The sample was expanded by the formula: Total number of permits (586) times the percentage of traditional fishermen in the sample (80/120) times the percentage of active traditional fishermen (27/80) in the sample [(586) (0.67) (0.34) = 132.51 ~ 133] equals the number of active traditional permittees in the study. The vessel price actually paid was adjusted by the Consumer Price Index to represent the value of the 133-vessel fleet in 1984.

To determine the annual mortgage cost associated with this fleet required three steps. The first and second steps determined the sampled fleet's value and expanded this figure to the entire fleet. The third step required assigning one mortgage rate to the entire fleet value. This assumed that this value would prevail for all vessels, and that all vessels would have a 10-year mortgage. After discussion with persons familiar with marine vessel mortgages and lending institution mortgage rates in central California, a rate of 12 percent[2] was felt to be a usable estimate.

Results

Who Was Contacted

As mentioned, attempts were made to contact only the traditional, non-Vietnamese fishermen. Of these 80, 16 permittees (20 percent) could not be located; 64 (80 percent) were contacted. Thirty-seven fishermen (46 percent) were not fishing setnets in the ocean between Point Sal and Point Reyes in

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[2] Personal communication with George Grundig, George M. Grundig and Assoc., 61 Moraga Way, 5, Orinda, CA 94563; and Michael Penzer, Bank of America, Box 37000, San Francisco, CA 94137.

1984. Twenty-seven fishermen (34 percent) were active in that area; however, only 23 (85 percent) of the 27 active fishermen were interviewed. One fisherman declined to be interviewed, and three were unavailable due to location or health. The following results and comments are based on the products of these 23 interviews and may not be representative of the entire traditional fleet nor are they in any way an indication of the magnitude of the Vietnamese setnet fishery in proportion, size or value.

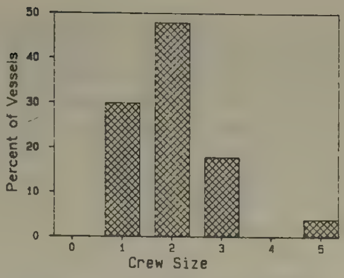

Figure 3.—Crew size (includes captain) of traditional central California setnet vessels in 1984.

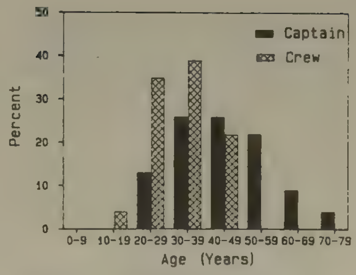

Figure 4.—Ages of captains and crew members on traditional central California setnet vessels in 1984.

Demographics of Fishermen

All except one of those interviewed were vessel captains. Three-fourths of them (17) were sole owners of their vessels, 8 percent (2) partly owned their vessels, and 17 percent (4) were nonowners. Crew size (including captain) averaged two people per vessel (range one to five). Vessels without crews (captain only) represented 30 percent of the fleet, 48 percent had two people, 18 percent had three, and 4 percent of the vessels had five people (Fig. 3).

Captains and crews of the vessels exhibited differences in age, education, and fishing experience. Captains averaged 45 years of age, with 14 years of education and 20 years of fishing experience. Crewmen averaged 31 years of age (Fig. 4), with 12 years each of education (Fig. 5) and fishing experience (Fig. 6). Over 80 percent of captains and crews were high school graduates. Forty-four percent of the captains had a post-high school education and 18 percent had a postgraduate education. Thirteen percent of the crewmen had post-high school education and none had postgraduate education.

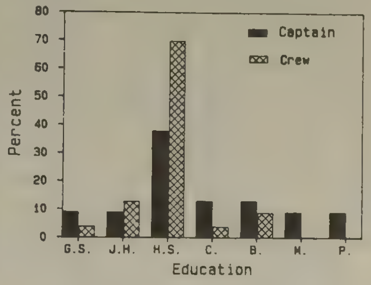

Figure 5.—Education of captains and crew members on traditional central California setnet vessels in 1984. G.S. = 3rd-8th grade; J.H. = 9th-11th grade; H.S. = high school; C. = some college; B. = bachelor's degree; M. = master's degree; P. = doctorate.

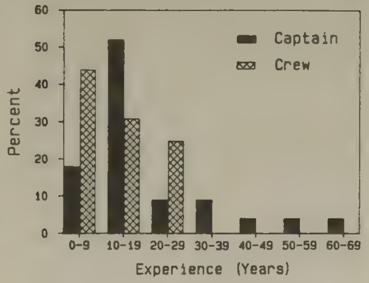

Figure 6.—Experience of captains and crew members on traditional central California setnet vessels in 1984.

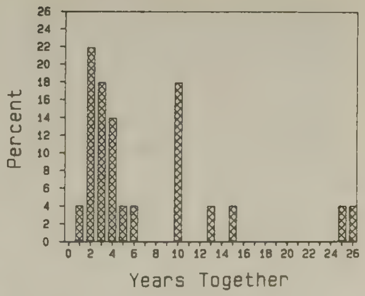

Figure 7.—Years captains and crew members on traditional central California setnet vessels have fished together through 1984.

One of the interesting aspects of the setnet fishery is the relationship between crew and captain. Most crewmen obtained the majority of their fishing experience with their current captain and averaged 7 years with this captain. Time spent with current skipper ranged from 1 to 26 years (Fig. 7), with 65 percent having had between 1 and 6 years with the current captain. The remaining 35 percent had been with the captain over 10 years. Sons of captains represented 13 percent of the total crewmen, and cousins 9 percent. All related crew members' fishing experience was gained with their relative and this experience averaged 10 years. The 78 percent of the crewmen not related to the captain averaged 6 years experience. Unrelated crew members who had fished with only one captain (17 percent of the total) averaged 2 years fishing experience. The unrelated crew members who had fished with more than one captain (61 percent of the total) averaged 8 years fishing with their current captain.

Gear Characteristics

Fishermen often fish with different nets during a given year. Neither the type of nets used nor the combination of nets appears to be related to fishermen's experience. Less than 10 percent of the fishermen stated that they fish with different types of nets during one trip. Seventy percent of the fishermen fish gill nets, 35 percent with trammel nets, and 43 percent with suspender nets. The total percentage exceeded 100 because some used more than one gear. Sixty-one percent used one gear only: Gill (35 percent), trammel (13 percent), and suspender (13 percent). Dual gear use was: Gill and trammel, 9 percent; gill and suspender, 17 percent; trammel and suspender, 4 percent; and all three net types, 9 percent.

Gill nets were grouped into three mesh-size categories: Small, 2⅛-3 inches; medium, 4¼-4⅜ inches; and large, 6-9 inches. The small-mesh nets are used to fish white croaker. The average effective fishing height of these nets (distance from floatrope [corkline] to footrope [leadline] when set) is 12 feet. The medium-mesh nets have an effective fishing height of between 12 and 18 feet and are used to fish rockfish, lingcod, and sablefish. Gillnets with the largest mesh have an effective fishing height of 16-22½ feet, and are used to catch rockfish, lingcod, starry flounder, *Platichthys stellatus*; and other flatfishes. These nets also can catch halibut and sharks, but are not considered optimal for these species.

Trammel nets have 8- to 10-inch mesh in the inner walls (81 percent were 8-inch) and 14- to 36-inch outer wall mesh (27 percent were 24-inch and 27 percent were 32-inch). The effective fishing height of these nets range from 6 to 18 feet (45 percent fished 18 feet). These nets are used to catch halibut, soupfin shark, *Galeorhinus zyopterus*, and other sharks, but rockfish, lingcod, and crabs are also caught.

Suspender nets have mesh sizes ranging from 7½ to 9½ inches, with 63 percent either 8 or 8½ inches. Effective fishing height ranges from 6 to 16 feet (30 percent fished 10 feet and 20 percent fished 15 feet). These nets are used to catch halibut, sharks, and rockfish, but other large fish are also caught.

Setnet netting is monofilament nylon and three-strand twisted nylon. Braided nylon was not being used, nor was multifilament nylon, although some fishermen indicated that they were going to build some multifilament nets, because of reports of less loss of captured fish.

All trammel nets were constructed of twisted three-strand nylon ranging in size from size 8 (0.038-inch diameter, 75-pound test) to size 16 (0.056-inch diameter, 135-pound test). Ninety percent of all suspender-net mesh was constructed of monofilament line from size 69 (19-pound test) to size 139 (28-pound test). Roughly half of the gill-net mesh was monofilament and the other half twisted three-strand nylon. Monofilament size was from 19-pound to 60-pound test line, while three-strand was between 50-pound and 170-pound test.

Anchors varied in type and weight among and between net types. The fishermen reported choice of type and weight to be a function of depth of water, length of net, time of year, and area of fishing.

Gill nets had the largest variety of anchor types (seven) and the largest weight range (24-90 pounds). The seven anchor types were Danforth[3] (35 percent), stock (23 percent), Northrop (12 percent), rocks (12 percent), cement blocks (6 percent), window heights (6 percent), and kedge (6 percent). Anchors used by trammel-net fishermen were the most homogenous: Danforth (80 percent), Northrup (10 percent), and kedge (10 percent).

Weight of trammel-net anchors ranged from 40 to 55 pounds (chain included). The average anchor weighed 51 pounds and 60 percent of the anchors weighed 55 pounds.

Suspender-net fishermen used Danforth or Northrop anchors 87 percent of the time and stock anchors the rest of the time. Anchors averaged 44 pounds and weights ranged from 30 to 80 pounds.

It appears that trammel-net fishermen have developed a coastwide consensus on the type and range of weights most suited for that gear. Suspender-net fishermen have the second smallest variance in anchors and appear to be adopting two types of anchors which weight about 40-45 pounds. Gill-net anchors, on the other hand, show no trend in type or weight. Fishing experience of the captain appeared to have little to do with either the anchor type or weight.

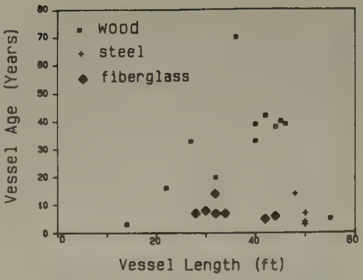

Figure 8.—Age of vessels vs. length relationship in the traditional central California setnet fishery in 1984.

All fishermen assembled their own nets. This generally requires the fishermen to attach premade netting or web to the footrope and floatrope and to attach bridles to the net for anchor, buoy, and flag. The fishermen's average annual assembly time for gill nets was 150 hours and for suspender and trammel nets 185 hours each. The gill net takes less time because only one item is attached to both foot- and floatropes.

Although obvious correlations were not found between types of setnet gear and fishermen's experience, age, or education, the gear used and the construction material of the vessel appeared to be correlated. Vessels were constructed of three materials: Wood (52 percent), fiberglass (30 percent), and steel (18 percent). Three-fourths of the wooden vessels were equipped with trammel and suspender nets and 58 percent with gill nets. Fiberglass and steel vessels were equipped with gill nets 82 percent of the time and trammel and suspender nets 55 percent. Vessel construction material was also correlated to vessel age. Wooden vessel ages ranged from 3 to 70 years, with an average of 31 years and a mode of 35. Fiberglass vessel age ranged from 5 to 14 years, with an average of 8 years and a mode of 7 years. Steel vessel ages ranged from 3 to 14 years with an average of 7 years and a mode of 6 years (Fig. 8). No significant correlation ($r = 0.36$; $P = 0.08$; $n = 23$) was found between vessel age and horsepower, but roughly three-fourths of the wooden and fiberglass vessels had diesel engines; the remainder were gasoline. All the steel vessels had diesel engines.

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[3] Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

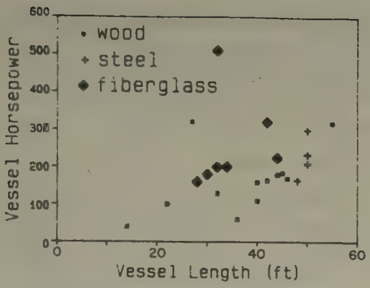

Figure 9.—Horsepower of vessels vs. length relationship in the traditional central California setnet fishery in 1984.

Engine horsepower averaged 155 for wooden, 227 for steel, and 256 for fiberglass vessels, but horsepower was not significantly correlated with vessel length ($r = 0.28$; $P = 0.19$; $n = 23$) or engine used (Fig. 9).[4] The hold capacity varied by construction material, with wooden vessel capacities averaging 13 tons (range from 0 to 30), fiberglass vessels 6 tons (range from 0 to 18), and steel vessels 28 tons (range from 15 to 30). No other obvious correlations between vessel characteristics, personnel, or gear were observed.

Characteristics of Fishing Operations

Many things affect the fishing operations of the setnet fishery. Included in these are fishing methods, kinship among fishermen, coastal mobility, and costs of fishing.

Fishermen using setnets off central California vary the length of time the nets are soaked, trip time, number of nets, length of nets, and method of fishing. These differences are in response to the species of fish being sought, weather conditions, vessel size, and time of the year. Most fishermen (96 percent) do not combine fishing methods during one trip. The remaining fishermen would use setnet and other gear, such as hook and line or traps. About one-fifth of the fishermen interviewed tended their nets and stayed in the area where the nets were set; the remaining fishermen (80 percent) set their nets and returned to port. Nets were generally set one day and pulled the next. Less than 10 percent of the vessels intentionally soaked the net longer than a day. When weather was bad, some nets would remain set until it was safe to retrieve. Fishermen generally avoided setting the net if the weather was too bad to retrieve or was believed to be turning bad. Trip length varied from 3 to 120 hours. A breakdown of trip length showed that almost two-thirds of the fishermen made trips of less than 2 days (0-12 hours = 18 percent; 12-24 hours = 23 percent; 24-48 hours = 23 percent). Eighteen percent of the fishermen made 3-day trips, 13 percent made 4-day trips, and 5 percent made 5-day trips.

Kinship is often an important aspect of a fishery and 70 percent of the captains in the setnet fishery had relatives in the fishing industry. All were male. Almost all of these relatives were fishermen, and most of them fished in central California. The remaining kin worked in the processing, wholesaling, or retailing sectors of the industry. Some fishermen purchased fish from other fishermen, and a few of these also processed fish for resale. A few purchased fish from other fishermen for another buyer, and some worked for a particular processor.

Mobility among fisheries and with a single fishery may decrease economic risk, allowing owners to fish where they believe economic returns will be the largest. Fishermen were asked to name their three most important fisheries. Seventy percent reported three fisheries, while 26 percent of the fishermen had participated in only two fisheries, and 4 percent in only one. Eleven fisheries were mentioned and the three most often reported were setnet fisheries for halibut (65 percent), Pacific herring, *Clupea harengus* (48 percent), and rockfish (42 percent). A total of six setnet fisheries was reported; the other three were shark (13 percent), white croaker (9 percent), and Pacific ocean perch, *Sebastes alutus* (4 percent). Other fisheries reported were round haul fishing with a lampara net for squid (13 percent) and chub mackerel, *Scomber japonicus* (13 percent), trolling for Pacific salmon, *Oncorhynchus* spp. (30 percent), trapping for Dungeness crab, *Cancer magister* (22 percent), and drift gillnetting for swordfish, *Xiphias gladius* (4 percent).

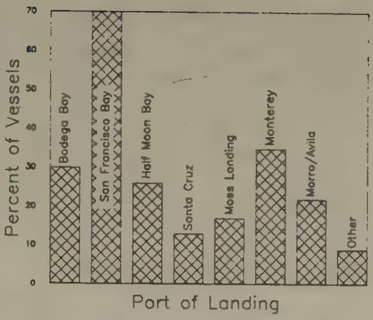

Figure 10.—Percentage of setnet vessels making landings in central California in 1984. Percentages do not equal 100 because vessels landed in more than one port.

Other gear used by 96 percent of the setnet fishermen was hook and line (70 percent-troll, longline, or pole), lampara net (30 percent), pots (20 percent—crab), and trawl (4 percent).

Setnet vessels not only fish in other fisheries and use other types of gear, but they also land at many different ports. Setnet fishermen in 1984 landed fish at only one port (22 percent of the fishermen), two ports (35 percent), three ports (31 percent), four ports (4 percent), five ports (4 percent), and six ports (4 percent). Landings were recorded in all ports from Bodega Bay to Avila Beach. Seventy percent of the vessels made landings in San Francisco, twice the percentage of any other port in the study area (Fig. 10).

Cost and Earnings

The costs of fishing are divided into two categories—fixed and variable. Fixed costs here include only the mortgage cost of the vessel. Variable costs include annual maintenance, repair and replacement of fishing nets, food, fuel, ice, insurance, vessel repair, vessel improvements, moorage, bookkeeping, and miscellaneous services. Crew remuneration could not be calculated from the data available.

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[4] When one observation was excluded, a significant correlation was found between vessel horsepower and length ($r = 0.49$: $P = 0.02$, $n = 22$).

Vessels' fixed costs were obtained by asking captains how much they actually paid for their vessels, how much they would sell their current vessel for, how much they would pay for a similar vessel, and how much it would cost to replace their vessel with a similar new one. The actual price and the willing-to-pay and willing-to-sell prices were all estimated to be near $10,000,000. This price is used as the surrogate for the total value of the 133 vessels in the calculated traditional fleet. The replacement price for the same vessels was estimated to be $15,000,000.

Fifty-seven percent of the surveyed vessels are mortgaged. Mortgages are held by private institutions (17 percent of all vessels), backed by government-guaranteed loans with private institutions (13 percent), or entail personal loans from relatives (17 percent) (no response 10 percent). Interest rates ranged from 8 to 13.2 percent, but 26 percent of all loans had no interest charge. These zero-interest loans required repayment in 2-4 years on a predetermined payment system. As previously noted, the traditional setnet fleet is valued at $10,000,000. If the entire fleet were mortgaged at 12 percent with a 10-year loan, the vessel owners would have an annual fixed cost of $1,750,000.

Although the total amount of the crews' remuneration could not be evaluated, the method was determined. Remuneration of setnet fishermen was generally on a lay (share) basis, which varied by vessel, area, ownership, fishery, and value of landing. Sixty percent of the fishermen were paid on a share of gross revenues, 36 percent on a shore of net revenues, and 4 percent were salaried. Crewmen receiving a shore of the gross revenue averaged 25 percent of the gross (range from 12 to 40 percent). Those receiving a share of the net revenue averaged 24 percent (range from 7.5 to 40 percent). Net revenue was determined by subtracting fuel and food from gross revenue. One vessel divided the food costs among owner and crew. Some crewmen received a higher percentage of the agreed-upon gross or net share when the revenues for the trip were low.

Table 1.—Minimum fixed and variable costs[1] attributed to setnetting in California, 1984.

Item	Costs		
Fixed cost of vessel:			
10-year mortgage at 12 percent			$1,750,000
Variable cost of fishing			
Moorage	$ 67,000		
Insurance	264,000		
Repair and other	158,000		
Improvements	115,000		
Fuel	355,000		
		$959,000	
Net material 1984		550,000	
Labor: 31,000 hr @ $8.07/hours		250,000	
Minimum variable cost			1,759,000
Minimum 1984 setnet fishing costs			$3,509,000

[1]Variable costs not included are crew remuneration and miscellaneous costs.

Seventy-eight percent of the captains made their entire income from fishing. The remaining captains earned between 40 and 80 percent of their income from fishing. Setnetting earnings comprised from 2 to 100 percent of captains' earnings, with 30 percent earning between 2 and 19 percent, 26 percent between 20 and 39 percent, 13 percent between 40 and 59 percent, 13 percent between 60 and 79 percent, and 18 percent between 80 and 100 percent.

The 1984 variable costs to the setnet fleet which I could attribute to moorage, insurance, repair, improvements, and fuel was nearly $1 million dollars (Table 1). Nets owned by the fleet were valued at $850,000. The cost of materials used to build or repair these nets in 1984 was $550,000. Building and repairing the setnets owned by the fleet took an estimated 31,000 hours of labor. This work is estimated to be worth $250,000 ($8.07/hour).[5] Other variable costs, such as ice, food, crew remunerations, bookkeeping, and miscellaneous services, could not be estimated from available data and, therefore, the variable cost should be considered a minimum. Minimum variable costs for 1984 would be about $1.8 million and total costs, variable plus fixed, would be about $3.5 million.

Ex-vessel Revenue

Three problems exist due to the incompatibility of the data base used to determine ex-vessel revenue and the area and scope of the study. One problem was caused because the ex-vessel values in PacFIN[6] for 1984 were not accurately differentiated by gear. Only 19 percent of the fish from the study area in the "net" and "other gear" categories were attributed to the "net" category. In 1985, 59 percent of the fish in these two categories were net-caught. Therefore, the species breakdown from the 1985 report rather than 1984 was used to determine catch by species.

Ex-vessel value estimates from 1984 data were not considered reliable because the "other gear" category accounted for over 90 percent of the landings in the Monterey area. How much of this could have been landed by setnets is not known. However, the total ex-vessel values of the "other gear" and "net" categories for 1984 and 1985 were only 8 percent apart and I believe that the 1985 ex-vessel value breakdown is similar to the 1984 value.

Another problem existed because the study site area was different from the PacFIN data. PacFIN uses the Pacific Marine Fishery Commission areas designated Conception and Monterey. This covers the area from the Mexican/California border north to lat. 40½°30′ N (roughly Cape Mendocino, Calif.). This northern boundary of the Monterey area is 150 n.mi. north of the study area, and the southern border of the Conception area is 260 n.mi. southeast of the study area.

A third problem was that only the traditional fishermen were sampled and PacFIN data covers both traditional and Vietnamese fishermen. The final problem entailed combining price and quantity information for the "other gear"

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[5] Blend of four 1984 hourly rate values. Hourly rate for a moderately-skilled government worker: GS-6 ($7.45), GS-7 (8.28). Weekly Federal Employers News Digest, Vol. 33, No. 36, 16 April 1984, Washington, D.C. Hourly rate for manufacturing total all categories: Humboldt County ($7.62), and San Francisco County ($11.38). 1985 County Business Patterns, U.S. Bureau of the Census, Wash., D.C.

[6] PacFIN is the Pacific Fishery Information Network data report published by the Pacific Marine Fishery Commission, Portland, Oreg.

Table 2.—California landings of "net" and "other gear" for the Pacific Marine Fishery Commission Monterey and Conception areas, 1984 (PacFIN[6] Report #009 and 054, 14 February 1985).

Species	Other gear			Net			Combined total	
	Qty. (mt)	Price ($/kg)	Value ($K)[1]	Qty. (mt)	Price ($/kg)	Value ($K)	Qty. (mt)	Value ($K)
Flatfish	60	$.93	$56	52	$1.00	$52	112	$108
Rockfish	1,804	.91	1,632	2,893	.84	2,425	4,697	4,057
Lingcod	171	.73	124	99	.69	68	270	192
Sablefish	307	.68	210	33	.46	15	340	225
Other	1	.71	1	1	.63	1	2	2
Misc. groundfish	37	1.76	65	128	1.55	198	165	263
California halibut	73	4.11	300	421	4.04	1,700	494	2,000
Total			$2,388			$4,459		$6,847

[1]K = 1,000.

Table 3.—Estimated[1] ex-vessel revenue attributed to traditional setnet fishermen in central California, 1985.

Species	Landings by other gear		Landing values			Value of traditional setnet fishery	
	Value[2] ($K)	Setnet (%)	Gear ($K)	Other net ($K)	Total setnet ($K)	% Total[4]	
Calif. halibut	$300	100	$300	$1,700	$2,000	100	$2,000
Flatfish	56	80	45	52	97	90	87
Rockfish	1,632	50	816	2,425	3,241	50	1,621
Lingcod	124	50	62	68	130	50	65
Sablefish	210	50	105	15	120	35	42
Other	1	50			1	100	1
Misc. groundfish	65	50	32	198	230	70	161
Total							$3,977

[1]Author's estimate; see text for other estimates.
[2]K = 1,000.
[3]Percentage of PacFIN report estimated to be made by setnets in study area from the "other gear" category.
[4]Percentage of adjusted landings attributed to traditional setnet fishermen.

category. Precision is lacking because only some of the fish in the "other gear" category were believed to be net-caught, and a price differential may have existed among gears within the "other gear" category.

The incompatible PacFIN and study data were adjusted after discussions with groundfish biologists[7] and industry people familiar with the breakdown of landings. The largest adjustments were to the rockfish in the PacFIN "other gear" category north of Bodega Bay and the sablefish and rockfish caught south of Santa Maria. Total value for these areas before adjustments was $6,847,000 (Table 2). Final estimates which have been adjusted for area, other gear landings, and Vietnamese landings resulted in an ex-vessel value for the traditional setnet fishermen of central California of $3,977,000 (Table 3). Due to the many adjustments, this figure was rounded to $4,000,000. Other scientists and fishermen were also contacted and their suggested adjustments resulted in total ex-vessel revenues of $4,309,000, $4,274,000, $4,070,00, and $3,776,000.

Conclusion

The traditional sector of the central California setnet fishery was calculated to support a highly educated and experienced group of 266 fishermen, fishing from 133 vessels for many different kinds of fish. The estimated cost, excluding crew remuneration and miscellaneous costs of the setnetting, is in excess of $3.5 million and the fishery produces an ex-vessel revenus of around $4 million. Setnet revenues represented an estimated 41 percent of the captain's total earnings from fishing in 1984. The value of vessels and setnet gear was about $11 million.

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U.S.-U.S.S.R. Discuss Bering Sea Fisheries

United States and Soviet fisheries delegations met in Washington, D.C., 18-22 April to discuss a broad range of fisheries issues of mutual concern. The U.S. side was headed by Ambassador Edward E. Wolfe, Deputy Assistant Secretary for Oceans and Fisheries Affairs, U.S. Department of State. The Soviet side was headed by V. K. Zilanov, U.S.S.R. Deputy Minister of Fisheries.

Both delegations characterized the talks as highly productive. Pursuant to the undertakings to improve fisheries relations contained in the Joint U.S.-Soviet Summit Statement made by President Reagan and General Secretary Gorbachev on 10 December 1987, in Washington, D.C., and the joint statement made by Secretary of State Schultz and Minister of Foreign Affairs Shevardnadze during their negotiations in February 1988, in Moscow, the two delegations considered possible ways for the two sides to act together on a wide range of issues related to conservation, rational utilization, and management of living marine resources.

Pursuant to understandings reached in Moscow in January 1988 to form a Bering Sea fisheries working group (see article below), the two delegations discussed the conservation aspects of Bering Sea fisheries in light of the vastly increased level of fishing in the region beyond the respective economic zones of the two states. A full exchange of views was made with regard to the legal, scientific, and enforcement aspects of the Bering Sea fisheries both within and beyond the respective economic zones of both states.

It was agreed that most of the commercially fished species of the Bering Sea are common to the economic zones of the United States and the Soviet Union while stocks of walleye pollock, *Theragra chalcogramma*, range both within and beyond the economic zones of the two states. Both sides expressed strong concerns over the adverse impact of unregulated, large-scale fisheries beyond the economic zones of pollock stocks which are a part of the ecological complex of the Bering Sea.

The delegations agreed on the need to develop further cooperation between the United States and the Soviet Union in the exercise of their rights and duties under international law to coordinate conservation and management of living marine resources of the Bering Sea. In addition, both sides agreed to convene jointly a scientific symposium in the United States in 1988, inviting scientists from all states concerned, to review the status of fishery resources in the Bering Sea, particularly pollock.

The two delegations agreed to continue coordinating the actions of both sides on fisheries of the Bering Sea. The two sides also discussed the implementation of the interim fisheries agreement, signed on 21 February by Secretary of State Shultz and Minister of Foreign Affairs Shevardnadze, regarding U.S. access to the U.S.S.R. economic zone. The two sides also considered the expeditious preparation and conclusion of a comprehensive fisheries agreement between the United States and the Soviet Union to govern their mutual relations in the field of fisheries. This agreement would, among other things, address conservation and management issues related to fishery resources of the Bering Sea, including the area beyond the respective economic zones of both states. Because of the urgency of these issues, the delegations agreed to continue bilateral discussions in Moscow in the near future. (Source: IFR-58/38.)

U.S.-U.S.S.R. Fishery Talks

United States and Soviet fishery delegations met in Moscow during 26-28 January 1988, to discuss a broad range of fishery issues of mutual concern. Both delegations characterized the talks as highly productive. It was agreed that the two sides would soon conclude arrangements allowing access by U.S. fishing vessels to the Economic Zone of the U.S.S.R. on the same terms as the U.S.S.R. vessels now have in the U.S. Exclusive Economic Zone, as provided in the current U.S.-U.S.S.R. Fisheries Agreement.

The two delegations also agreed to immediately form a bilateral U.S.-U.S.S.R. Working Group on Fisheries of the Bering Sea. This group will include legal, scientific, and technical specialists from both sides which will develop recommendations for dealing with increased fishing in the Bering Sea. The talks included finalizing plans for a March industry-to-industry meeting in the Soviet Union to discuss possible fishery commercial joint ventures, and plans to address additional scientific and other issues to improve overall bilateral fisheries cooperation on a mutually beneficial and equitable basis.

U.S. Ends Certification of U.S.S.R. for Whaling

U.S. Secretary of Commerce C. William Verity has announced his decision to terminate the certification of the Soviet Union under the Packwood-Magnuson and Pelly Amendments for its whaling practices. The announcement was made in Moscow on 14 April during a press briefing at the end of the Joint Commercial Council (JCC) meeting, as follows:

"In concluding my remarks, I want to announce that I have received assurances from the Soviet Ambassador to the United States confirming that the Soviet Union has ceased commercial whaling and intends to work through the International Whaling Commission (IWC) for whale research and conservation. The cessation of commercial whaling by whaling nations has been a major objective of global environmental groups and the IWC, supported by the United States. I welcome the Soviet decision and hope that it sets a pattern for similar decisions on the part of other whaling nations to work within the IWC for the purposes of research and conservation. We look forward to cooperating more closely with our Soviet colleagues in the IWC, our fisheries relations, and our broader bilateral agenda."

Secretary Verity sent a letter to U.S. Secretary of State George P. Shultz conveying his decision (see below). A *Federal Register* notice, required by law, explaining the reasons for his decision was also prepared for publication on 14 April (see below). The Secretary of Commerce has withdrawn the certification because the reasons for the April 1985 certification no longer prevail. The Soviet Union has confirmed that it has ceased whaling and intends to work through the IWC for whale research conservation. (Source: U.S. Embassy, Moscow).

Text of letter to Secretary George P. Shultz relating Commerce decision to terminate the certification of the Soviet Union for whaling practices:

Dear George, On April 1, 1985, Secretary of Commerce Malcolm Baldrige certified to the President that Nationals of the Soviet Union were conducting whaling operations that diminished the effectiveness of an international fishery conservation program under the Pelly Amendment to the Fishermen's Protective Act of 1967, 22 U.S.C. 1978 (1983 SUPP.) and the Packwood-Magnuson Amendment to the Magnuson Fishery Conservation and Management Act, 16 U.S.C. 1821 (1983 SUPP.). Following certification and consultations between the Departments of State and Commerce, Soviet fish allocations were reduced by 50 percent and all allocation available to the Soviet Union eliminated one year later. The Pelly Amendment requires periodic review of the basis for certification, and I have recently concluded such a review. I have determined that the conditions that prompted the certification of the Soviet Union no longer exist, and I am terminating the certification under both the Pelly and Packwood-Magnuson Amendments. I recommend that the Department of State promptly notify the Government of the Soviet Union of the termination of the certification. In addition, the National Oceanic and Atmospheric Administration will provide recommendations for fish allocations to be made available to the Soviet Union at the appropriate time. Sincerely, Secretary of Commerce.

Federal Register notice explaining the termination of Soviet certification.

Summary: Notice is published that the Secretary of Commerce finds the reasons for the certification of the Soviet Union, under the Pelly and Packwood-Magnuson Amendments for activities that diminish the effectiveness of an International Fishery Conservation Program, no longer prevail and that the certification has been terminated.

Supplementary Information: Under the Pelly Amendment to the Fishermen's Protective Act and the Packwood-Magnuson Amendment to the Magnuson Fishery Conservation and Management Act, the Secretary is responsible for determining if nationals of a foreign country, directly or indirectly, are conducting fishing operations in a manner or under circumstances which diminish the effectiveness of an international fishery conservation program. If the Secretary of Commerce so determines, such certification is reported to the President. On April 1, 1985, Secretary Malcolm Baldrige certified to President Reagan that the Soviet take of Southern Hemisphere minke whales had diminished the effectiveness of the International Whaling Commission (IWC) conservation program. The Secretary based his determination on the following facts: 2) The Soviet harvest of Southern Hemisphere minke whales was greater than the level the United States considered the U.S.S.R.'s traditional share, 2) The 1984-85 IWC quota for Southern Hemisphere minke whales was exceeded due to Soviet harvest and 3) there had been no indication that Soviets intended to comply with IWC standards.

The Soviet Union has ended its commercial harvest for Southern Hemisphere minke whales and has indicated its intention to cooperate in the conservation of whales within the framework of the IWC. Given that the reasons for the certification of the Soviet Union no longer prevail, the Secretary has terminated the certification under both the Pelly and Packwood-Magnuson Amendments. (Source: IFR-88/31.)

U.S., U.S.S.R. Sign Fisheries Agreement

A comprehensive agreement governing fisheries relations between the United States and the U.S.S.R. was completed on 23 May after a week-long negotiating session in Moscow; it was signed at the Moscow Summit on 31 May. The agreement provides for access by each nation's fishing vessels to surplus fishery resources in the other's Exclusive Economic Zone. Fishing vessels of both nations also can purchase supplies, effect repairs, and exchange crews at specified ports: Boston, Mass., Portland and Astoria, Oreg., and Dutch Harbor, Alaska, in the United States; Murmansk, Provideniya, Korf, and Oktyabrski in the Soviet Union.

The agreement states that the two countries have a common concern for conservation of shared stocks in the Bering Sea and for Pacific salmon, *Oncorhynchus* spp., resources, and will cooperate in data collection and scientific research. The agreement also provides for the establishment of a bilateral consultative committee to meet each year, and for the appointment of a U.S. fisheries attache at the U.S. Embassy in the Soviet Union. As an adjunct to the negotiation of this agreement, the two sides agreed to hold an international scientific symposium on Bering Sea walleye pollock, *Theragra chalcogramma*, resources to be held in Sitka, Alaska, in mid-July, and agreed to coordinate efforts to achieve third-party cooperation in conserving pollock resources.

NMFS Will Enforce Lacey Act in Bahamian Waters

It is illegal to possess fish or lobster taken in Bahamian waters, or to import them into U.S. jurisdiction, or to sell them in the United States or to a foreign interest, or to attempt to import or sell them, Joseph Angelovic, Acting Southeast Regional Director of the National Marine Fisheries Service announced early this year. The Bahamas exercises fisheries jurisdiction over all waters to the East of the Fishery Conservation Zone/Exclusive Economic Zone line between Florida and the Bahamas depicted on U.S. chart 11460, 28th Edition, Feb. 22, 1986.

To clear up any possible confusion Angelovic stated, let it be known that any U.S. fisherman found fishing in Bahamian waters will be prosecuted by the National Marine Fisheries Service to the fullest extent of the law under the Federal Lacey Act. Penalties for felony conviction are up to 5 years in prison and up to $20,000 fine, plus loss of all fish taken, the vessel, trailer, vehicle, and equipment used to aid in the violation for most violations. Penalties for a misdemeanor conviction are up to 1 year in prison and up to a $10,000 fine, while civil penalties of up to $10,000 penalty per violation can be assessed. For further information or to report violations, contact Eugene Proulx at (813) 893-3145.

U.S. Fishery Export Picture Looks Good

The year 1987 was a banner year for U.S. fish exporters, with total overseas sales of fishery products a record $1.66 billion, up 22 percent over 1986, according to the National Oceanic and Atmospheric Administration (NOAA). NOAA said American joint-venture operations also set records last year. Exports and joint ventures in 1987 together amounted to more than $1.8 billion. Joint ventures are those in which U.S. fishermen sell their catch at sea to foreign processing boats.

According to NOAA economists, if this trend continues, fish sales to foreign buyers will top $2 billion this year, making the United States the world's biggest fish exporter. The volume of the catch rose too, to a record 525,000 metric tons, up 13 percent from 1986, the Commerce Department agency said. And the country's biggest foreign fish buyer, Japan, bought fish and fishery products worth a record $1.074 billion in 1987.

Also in 1987, seafood imports rose by $800 million to a record $5.6 billion. If nonedible marine products are included—mostly high value-added jewelry made with coral or pearls—that import figure increases to $7.9 billion. NOAA says it expects the 1988 balance-of-trade figures to look about the same. Part of the reason for the persistent trade deficit, says NOAA, is that the U.S. fishing industry cannot fully supply America's growing taste for high-priced products like shrimp, tuna, scallops, lobster, and farmed salmon. That demand is being met by imports.

NOAA Moves to Cut Dolphin Deaths

Foreign nations exporting yellowfin tuna to the United States caught in the eastern tropical Pacific Ocean must take steps to reduce the number of dolphins killed during purse seine fishing, the Commerce Department's National Oceanic and Atmospheric Administration (NOAA) announced early this year. Countries that do not reduce dolphin deaths will not be allowed to import yellowfin into the United States.

A new ruling by NOAA's National Marine Fisheries Service, requires foreign fleets that catch yellowfin tuna from purse seine vessels to establish regulations comparable to those required for the U.S. fleet. The ruling, which went into effect in mid-April, requires observers to monitor fishing activities and the use of gear and techniques that minimize harm to dolphins during yellowfin fishing. The ruling also requires that by 1991, the average annual rate of dolphins killed by a foreign fleet in the area is comparable to the yearly rate for the U.S. fleet.

Eight foreign nations, including Mexico, Venezuela, and Ecuador, fish for yellowfin in the eastern tropical Pacific. In 1986 they harvested almost 195,000 tons of fish. More than 46,000 tons, worth an estimated $35 million, was exported to the United States. In the eastern tropical Pacific where schools of yellowfin tuna swim beneath dolphin herds, fishermen search for schools of dolphins as an indication of tuna. The fishermen encircle both dolphins and tuna with huge purse seine nets. Although the vast majority of the dolphins escape or are released by fishermen, a few become entangled and drown.

NOAA Ship *Researcher* Is Renamed *Malcolm Baldrige* to Honor Late Commerce Department Secretary

The NOAA Ship *Researcher*, an oceanic research vessel operated by the Department of Commerce's National Oceanic and Atmospheric Administration (NOAA), was renamed the NOAA Ship *Malcolm Baldrige* on 1 March in honor of the late Commerce Secretary. Mrs. Baldrige participated in the renaming ceremony, hosted by Commerce Secretary C. William Verity, which began at 11 a.m. at the Washington Navy Yard, Pier 1. The ship was renamed *Malcolm Baldrige* in recognition of the late Commerce Secretary's public service to the Nation. Secretary Baldrige died in a rodeo accident 26 July 1987.

The 2,963-ton, 278-foot *Researcher/ Baldrige*, the largest east coast ship in NOAA's fleet of 23 research and survey ships, conducts climate research in the Atlantic Ocean and Caribbean Sea. The ship is based at NOAA's National Ocean Service Atlantic Marine Center in Norfolk, Va., and operates out of NOAA's ship support base in Miami, Fla. The ship can carry 82 NOAA Corps officers, civilian crew members, and visiting scientists, and is equipped with a scientific laboratory, sophisticated communications and computer systems, and the latest scientific instruments for making environmental measurements at sea.

The ship was built by the Toledo Plant of the American Shipbuilding Company and launched on 5 October 1968. It has two 1,600-horsepower, geared diesel engines that power twin controllable-pitch screws and a 450-horsepower bow thruster that can be used to move the ship at very slow speeds or hold it steady on a position. With a cruising range of 13,000 n.mi. and a cruising speed of 14.5 knots, the ship can carry

6-month's worth of provisions for extended scientific operations in remote ocean areas, and can remain at sea for more than a month at a time.

New Federal Lobster Regulations Announced

New Federal regulations governing the American lobster fishery became effective on 31 December 1987. These new regulations were developed by the New England Fishery Management Council in cooperation with the lobster-producing states in New England and the Middle Atlantic. The regulations 1) increase the minimum carapace length for lobsters, 2) prohibit the possession of V-notched lobsters throughout the range of the stock, 3) implement a nationwide prohibition on the possession of V-notched and egg-bearing female lobsters and all lobsters smaller than the minimum carapace length taken and retained in violation of the Magnuson Fishery Conservation and Management Act, and 4) revise the gear identification/marketing requirement.

The minimum carapace length is scheduled to be increased from $3\frac{3}{16}$ inches to $3\frac{5}{16}$ inches by increments of $\frac{1}{32}$ of an inch per year over a 5-year period. An escape vent size increase is scheduled to take place at the mid-point of the carapace length increases. The new vent size will be compatible with a minimum carapace length of $3\frac{5}{16}$ inches. The industry will be notified before the end of 1988 as to the exact specification of the new venting requirement. Effective dates of the scheduled increases in carapace length are as follows:

Date	Minimum carapace length
1 January 1988	$3\frac{7}{32}$ inches
1 January 1989	$3\frac{1}{4}$ inches
1 January 1990	Escape vent size to be compatible with a minimum carapace length of $3\frac{5}{16}$ inches
1 January 1991	$3\frac{9}{32}$ inches
1 January 1992	$3\frac{5}{16}$ inches

Following each length increase, dealers and wholesalers will have a 180-day grace period to dispose of lobsters purchased or received in the prior year which do not meet the new minimum carapace length.

Secondly, these new regulations prohibit nationwide the possession of egg-bearing lobsters, V-notched female lobsters, and lobsters smaller than the minimum carapace length that were taken and retained in violation of the Magnuson Act. The possession prohibition applies to all lobsters found in commerce unless it can be shown that the lobsters were 1) imported, or 2) harvested by a vessel fishing exclusively in state waters, in which case regulations of the state will prevail. Lobsters from a vessel holding a Federal fishing permit, or a state permit that is endorsed for Federal waters, will be presumed to have been harvested from the Federal waters and will be subject to these new Federal regulations.

Lastly, these regulations revise the gear identification/marking requirement to provide increased flexibility. In addition to allowing Federal Permit Holders to use their state gear identification/marking system, the new regulations authorize gear to be marked with a "number assigned by the Regional Director" instead of simply "the Federal Fishery Permit Number." This means that gear may be marked with the vessel's 1) Federal Fishery Permit, 2) Official or Documentation Number, or 3) any number as authorized by letter from the Regional Director. For additional information on these new Federal regulations, contact Carol Kilbride of the National Marine Fisheries Service at (617) 281-3600.

Oyster Resource Disaster Aid

A total of $2.0 million was made available by late last year under the resource disaster provisions of the Commercial Fisheries Research and Development Act (P.L. 88-309) to the states of Delaware, Maryland, New Jersey, and Virginia, to assist in restoring the commercial oyster fisheries in Chesapeake and Delaware Bays, the NMFS Northeast Regional Office reported in December. Continuation of drought conditions experienced by the Mid-Atlantic states resulted in increased Bay salinities and, unfortunately, a favorable environment for spread of the haplosporidian parasite, commonly known as MSX. As a result, high mortalities and reductions of over 40 percent in yield of marketable oysters occurred, and adverse resource conditions could continue through 1990. Activities being conducted by the four states include dredging and planting of oyster shell for propagation purposes, and field trials of disease resistant strains.

Tagged U.S. Salmon Recovered in Greenland

NMFS Northeast Fisheries Center scientists, in cooperation with their Canadian and Danish counterparts, detected 146 coded-wire-tagged Atlantic salmon, *Salmo salar*, among over 25,000 salmon examined at four West Greenland fishing ports during August and September 1987. Of the 146 tagged fish, 82 were of U.S. origin, 19 of Canadian origin, and the rest of European origin (mostly England, Wales, and Ireland). Of the U.S.-origin tagged fish, 77, or 94 percent, were from Maine rivers. These tag recoveries are particularly significant because they represent the first year in which coded-wire-tagged salmon of Maine origin have been available to the West Greenland fishery.

Scientists examined the salmon after the fish had been bought by fish processors, but before the fish had been flash frozen and glazed. Scientists used special metal detectors to identify which salmon had the magnetically coded, 1 mm wire tags imbedded in their skulls. These coded-wire tags, which are undetectable by fishermen and thus necessitate the special sampling by scientists, are now in common use by the salmon-producing countries of the North Atlantic. The United States began applying these tags to 1-year-old salmon (smolts) in 1985.

Marine Debris Conference Slated for Hawaii, 1989

The Second International Conference on Marine Debris is scheduled for 2-7 April 1989 in Honolulu, Hawaii, according to Richard S. Shomura, Chairman. Sponsors are the National Marine Fisheries Service, the Marine Mammal

Commission, and the University of Hawaii's Sea Grant College Program.

Since the first (1984) international "Workshop on the Fate and Impact of Marine Debris," also held in Honolulu, a substantial body of information on the topic has been amassed, heightening scientific, legal, and political recognition of the problem. The second conference, says Shomura, is intended to provide a forum to present and evaluate the various aspects of the problem and potential solutions. Some of the topics to be covered include: New data on the types, amounts, sources, fates, and distribution of marine debris in different ocean areas; existing and potential methods for data collection; nature and extent of impacts on living marine resources; impacts on human health and safety of ships at sea; aesthetic and other impacts on coastal environments; effectiveness and future role of programs educating the public and promoting awareness of the problem; and programs necessary to assess the effectiveness of measures addressing the problem.

Early registration fee is US$125 (US$150 at the conference). Further information for prospective authors and participants is available from Richard S. Shomura, Conference Chairman, NMFS Honolulu Laboratory, 2570 Dole Street, Honolulu, HI 95822-2396 U.S.A. (telephone 808-943-1229; or telegram MDEBRIS; or Telex 6503504141 MCI UW).

Mackerel Spawn Heavily North of U.S. Border

Spawning by Atlantic mackerel, *Scomber scombrus*, was more intense in Canadian waters than in U.S. waters during the 1987 spawning season. That's a preliminary observation resulting from eight egg-and-larval surveys conducted by NMFS Northeast Fisheries Center scientists during late spring and early summer as part of a cooperative U.S., Canadian, and Polish effort to estimate the spawning stock biomass of Northwest Atlantic mackerel.

Detailed analysis of the surveys' samples and data shows that spawners in Canadian waters accounted for 89 percent of the adult spawning biomass; spawners in U.S. waters accounted for 11 percent. The Center's estimate of 1987 adult spawning biomass—based on these egg surveys—is 1.10 million metric tons (2.47 billion pounds). This estimate compares very favorably with estimates based on virtual population analysis.

Northwest Atlantic mackerel total stock biomass, as estimated by virtual population analysis, has fluctuated widely over the past 25 years. (Estimates of total stock biomass will always be somewhat larger than estimates of adult spawning biomass since the former includes all age 1 and older fish, whereas the latter includes hardly any age 1, a variable proportion of age 2, and almost all age 3 and older fish.) Total stock biomass increased from 0.30 million metric tons (0.67 billion pounds) in 1962-65 to 1.9 million metric tons (4.26 billion pounds) in 1970-71, decreased to an average of 0.49 million metric tons (1.09 billion pounds) in 1977-81, and increased to 1.50 million metric tons (3.36 billion pounds) in 1986.

Fish Processing Waste Effective as Fertilizer

NMFS Gloucester Laboratory experiments show that fish hydrolysate (a liquified fish mixture derived from the solid wastes of fish processing) is an effective plant fertilizer. This finding offers a possible solution to the recurring problem encountered by fish processors on how to dispose effectively, efficiently, and safely of the solid wastes from fish processing operations. This problem currently limits the restoration, maintenance, or growth of several commercial fishing ports in the U.S. northeast region.

Scientists compared fish hydrolysate that was made from Atlantic cod, *Gadus morhua*, "frames" (what's left after filetting) and that roughly had a 3-5-1 fertilizer value (percent content of nitrogen, phosphorous, and potassium), with a well-known commercial fertilizer with a stated 20-20-20 value. Under controlled but variable conditions of soil type, fertilizer concentration, and fertilization frequency, the fish hydrolysate increased yields in the test crop—greenhouse jalapeno peppers—from 20 to 123 percent.

Cooperative Ocean Cruise Seeks Data on Armorhead

Scientists from the NMFS Southwest Fisheries Center's Honolulu Laboratory returned in February from a 30-day cruise aboard the *Townsend Cromwell* collecting biological and oceanographic information from waters over and surrounding the Southeast Hancock Seamount, which is located about 200 n.mi. northwest of the Hawaiian Archipelago and just within the U.S. 200-mile Exclusive Economic Zone (EEZ).

"From a historical standpoint, the results would hopefully provide valuable insight into what once was a viable commercial fishery for Soviet and Japanese fishing ventures," said Richard S. Shomura, Director of the NMFS Honolulu Laboratory. Shomura added that the seamounts provided habitat for large concentrations of fishes, in particular the target species of fish known as the pelagic armorhead. In the spring of 1985, when armorhead were nearly exhausted by the fishing pressure applied by foreign vessels, the NMFS closed the seamounts within the EEZ to all foreign fishing. The Honolulu Laboratory has since continued to monitor and explore the dynamics associated with abrupt topographical features such as the seamounts present. Chief Scientist Michael P. Seki reported that fishery operations on the cruise involved primarily bottom longlines and bottom trawling gear. Collection of oceanographic data involved sampling along predetermined transects with such equipment as an acoustic Doppler current profiler, a geomagnetic electrokinetograph, hydroacoustic echo sounders, various small nets, etc.

In addition to Seki, scientific personnel on the cruise were research assistants Russell Y. Ito, Frank A. Parrish, Dennis Therry, and Christopher D. Wilson. Also participating on the cruise were cooperating scientists Jed Hirota and James Finn from the University of Hawaii Department of Oceanography, and Peter Koske and Thorsten Knutz from Kiel University in the Federal Republic of Germany.

Predation Limiting Hard Clam Production

Predation substantially limits the production of hard clams in Great South and Barnegat Bays, the largest clam production areas in New York and New Jersey, respectively. These findings come from separate field studies of these areas by NMFS Northeast Fisheries Center scientists, supplemented by laboratory experiments also conducted by the Center.

The Barnegat Bay field study was conducted in conjunction with a cooperative effort to create hard clam spawning sanctuaries throughout the Bay. At each of five study sites, scientists planted paint-marked juveniles (5 mm long) clams around stakes. At four of the five sites, there was at least 62 percent mortality of marked clams within 70 days, with most of it due to crab predation, although at one of those four sites, almost half of the predation was due to oyster drills. In the most extreme case, 96 percent of the marked clams at one site were crushed after four days, indicating crab predation.

In the Great South Bay field study, a scuba-deployed hydraulic suction sampler was used to collect clams at four sites in August 1986, and at six sites in August 1987. This 2-year effort permitted scientists to follow the mortality and growth of the Bay's strong 1985 "set" of clams. Between 1986 and 1987, the average density of these clams decreased from ten to three per square yard. We attribute the mortality largely to predation, mostly by crabs. (Incidentally, in 1987, when the 1985-set clams were 5-20 mm long, we found no other abundant size classes less than 40 mm long. Consequently, clam harvests in the Bay should decrease for 2 or more years until the 1985-set clams grow to a commercial size.)

Scientists also ran a laboratory experiment to evaluate the predation potential of sand shrimp and grass shrimp—which are often abundant on clam beds—on early-stage juvenile hard clams. Individual shrimp were placed in dishes which held 50 1 mm-long clams. In every case, all clams were consumed in 24 hours. The results of the field studies and laboratory experiments show the importance of predation in limiting hard clam production in the New York-New Jersey area.

Toxic Mackerel Liver Eyed in Whale Deaths

In response to the known deaths of 14 humpback, 4 minke, and 2 fin whales along the New England coast in December and January, the NMFS Northeast Fisheries Center began testing the toxicity of liver extracts from several fish species known to be prey—as juvenile or adults—of whales. On 18 December 1987 Center scientists found liver extracts from Atlantic mackerel to be toxic to laboratory test mice. Subsequent evidence gathered by the Center and other organizations has now implicated the consumption of mackerel containing paralytic shellfish toxins in the whale deaths.

Relatively low levels of toxicity were found in all mackerel liver extracts from samples collected within the western Atlantic range of this species (i.e., from Northumberland Strait in the Gulf of St. Lawrence to the Mid-Atlantic region). Mean toxicity levels were 185 μg of toxin per 100 g of liver, with up to 446 μg/100 g present in some samples. Interestingly, scientists found toxicity levels of 60 μg/100 g in liver extract from mackerel stomachs collected off Nantucket Island as long ago as April 1986. It is emphasized, however, that there is no danger to human consumption of mackerel as no toxicity has been detected in the muscle tissue, the edible portion.

No toxicity has been detected in the livers of other whale prey species such as Atlantic herring and silver hake (whiting), nor in the liver of goosefish (monkfish). Stomach contents of one whale—consisting mostly of bones—were tested and found to be only mildly toxic, causing delayed death of mice.

Baseline Established for 12-Mile Dumpsite

The NMFS Northeast Fisheries Center has now completed the first year and a half of sampling at the New York Bight's 12-Mile Dumpsite. The sampling to date has been designed to establish a baseline for determining the effects—primarily biological—of ending sewage-sludge dumping at the site. (The last dumping was in December 1987.)

With a year and a half of sampling completed, scientists can now begin to compare any seasonal trends. During the November survey of three stations, chosen to represent impacted, enriched, and less polluted habitats, some trends persisted from autumn 1986 to autumn 1987. The dominant bottom fishes were little skate (75 percent of the weight tow in 1986; 50 percent in 1987) and winter founder (19 percent in 1986; 15 percent in 1987). At the "impacted" station, the average weight per tow for all bottom fishes increased from 22 to 40 pounds. The dominant crustaceans were rock and horseshoe crabs which ranked first and second, respectively, in weight per tow for both 1986 and 1987. At all three stations though, the weight per tow decreased for both species between the two years.

These early comparisons, however, do not statistically indicate that any rapid significant shift from crustaceans to fishes has occurred. Continued sampling will be necessary to determine if any changes in the biological community in and around the site are related to the ending of sewage-sludge dumping.

Scientists Studying Seafloor Megaplumes

National Oceanic and Atmospheric Administration (NOAA) scientists are studying the origins of a geological process that sends massive amounts of hot fluids into the ocean from cracks in the seafloor. Called megaplumes, the rich, hot soup of mineral grains and dissolved minerals and gases can be miles wide and may have a major influence on ocean chemistry, according to Edward T. Baker of NOAA's Pacific Marine Environmental Laboratory in Seattle, Wash. The Commerce Department scientist said the process, caused by tectonic or volcanic activity suggests a geologic activity different from that which causes the continuous leaking of hot fluid from seafloor thermal vents.

The existence of the process was suggested a year ago when researchers aboard a NOAA ship, investigating seafloor venting along the Juan de Fuca Ridge off the Washington and Oregon coasts, discovered a huge, circular plume of hot water floating deep in the ocean. It was about 10-12 miles in diameter and more than a quarter-mile deep. Last September, again over the Ridge, investigators found a recurrence of megaplume activity.

"It closely resembled the original megaplume, formed by the expulsion over a period of a few days of hundred of millions of tons of superheated seawater from seafloor cracks," Baker said. Since September, he and colleagues Gary Massoth and Richard Feely have analyzed samples from the megaplume, finding them rich in silica, manganese, and iron leached by hot seawater from rocks in the ocean crust. They believe the phenomenon could be common in ocean areas where the seafloor is similar to that of the Pacific ridge.

Juan de Fuca Ridge is a seafloor spreading center where lava from the earth's core rises to form a new ocean crust as the North American and Pacific crustal plates separate. This seafloor spreading creates slow, steady venting of superheated seawater at many locations in the area. The program, called Vents, has studied the phenomenon for 3 years to understand its effect on ocean chemistry. The program operates at the Hatfield-Oregon State University Marine Science Center in Newport, Oreg.

1986-1987 Warmest Years Since 1953

The years 1986 and 1987 were the warmest two years in the contiguous 48 states since 1953, with only three fractionally warmer years this century (1934, 1931, and 1921), according to scorekeepers at the National Oceanic and Atmospheric Administration's (NOAA) National Climatic Data Center (NCDC), Asheville, N.C. Average annual temperature for the two years was 54°F. Back-to-back warm years last occurred in 1953-54, with average temperatures of 54.7 and 53.9 degrees. The spring of 1986 was warm throughout the 48 contiguous states. The warmth of 1987 was especially noteworthy during the winter of 1986-87 and the spring of 1987 in the north central portions of the country, the Commerce Department agency reports.

	Winter 1985-86	Spring 1986	Summer 1986	Fall 1986
W	2nd warmest	7th warmest	12th warmest	21st coldest
NW	41st coldest	11th warmest	6th warmest	41st coldest
SW	4th warmest	4th warmest	22nd warmest	24th coldest
WNC	22nd warmest	4th warmest	18th warmest	20th coldest
S	25th warmest	7th warmest	42rd warmest	42nd coldest
ENC	24th coldest	5th warmest	37th coldest	22nd coldest
C	27 coldest	9th warmest	40th warmest	39th warmest
SE	40th coldest	36th warmest	9th warmest	8th warmest
NE	37th coldest	6th warmest	15th coldest	17th coldest
	Winter 1986-87	Spring 1987	Summer 1987	Fall 1987
W	40th warmest	5th warmest	42nd warmest	3rd warmest
NW	28th warmest	4th warmest	30th warmest	2nd warmest
SW	36th warmest	28 warmest	42nd coldest	24th warmest
WNC	the warmest	3rd warmest	35th warmest	12th warmest
S	35th warmest	42rd coldest	36th coldest	27th coldest
ENC	the warmest	2nd warmest	9th warmest	45th warmest
C	25th warmest	7th warmest	13th warmest	27th coldest
SE	41st coldest	33rd coldest	7th warmest	12th coldest
NE	42nd warmest	9th warmest	25th warmest	22nd coldest

Following is a breakdown by regions comparing each season of the recent two-year period with NCDC's records going back to 1895. Regions consist of the following states: West (W) = California and Nevada; Northwest (NW) = Idaho, Oregon, and Washington; Southwest (SW) = Arizona, Colorado, New Mexico, and Utah; West North Central (WNC) = Montana, North Dakota, Nebraska, South Dakota, and Wyoming; and South (S) = Arkansas, Kansas, Louisiana, Mississippi, Oklahoma, and Texas; East North Central (ENC) = Iowa, Michigan, Minnesota, and Wisconsin; Central (C) = Illinois, Indiana, Kentucky, Missouri, Tennessee, West Virginia, and Ohio; Southeast (SE) = Alabama, Georgia, Florida, North Carolina, South Carolina, and Virginia; and Northeast (NE) = Connecticut, Delaware, Massachusetts, Maryland, New Hampshire, New York, Pennsylvania, Rhode Island, Vermont, Maine, and New Jersey.

Seasons are defined as: Winter = December, January, and February; Spring = March, April, and May; Summer = June, July, August; Fall = September, October, and November.

Crab Analog Made From Pacific Whiting Surimi

The Utilization Research Division of the NMFS Northwest and Alaska Fisheries Center reports that it has successfully processed crab analog using Pacific whiting surimi. The surimi was produced during August and October 1987 using ocean-caught fish, and was processed into the analog in a production run at a commercial plan in January 1988. Successful production of the crab analog was made possible by the incorporation of an inhibitor for the protease enzyme(s) present in Pacific whiting parasitized by the myxosporean *Kudoa* sp. The run of analog in the commercial plant consisted of 100 percent Pacific whiting surimi. No processing problems were encountered in any of the production steps.

Acceptability of the finished product is comparable to product prepared from Alaska pollock surimi. The product has been served to several groups familiar with the technical properties of surimi and analog products. One of these groups was the Pacific Fisheries Technologists at the annual meeting in February 1988. Without exception, everyone that tasted the product agreed that it is excellent and completely acceptable. This demonstrates the feasibility of using Pacific whiting for surimi from which crab analogs and similar type products can be fabricated.

A common method of measuring the quality of surimi for use in analog preparation is to determine gel strength of kamaboko prepared from the surimi. The gel strengths of kamaboko prepared from the two lots of surimi used in this commercial run were as follows:

	Gel strength	
Pacific whiting surimi lot	Control (no inhibitor)	Inhibitor added
August 1987	82.3	763.8
October 1987	36.0	722.3

The effect of inhibitor addition is obvious. The gel strength is increased 10 times or more. A gel strength of about 650 is needed to make a high quality analog product.

Yellowfin, Bigeye Tuna Tagging Program Underway

A forward-looking group of U.S. east coast sportfishermen, charter boat captains, and sportfishing clubs have joined leading tackle manufacturers, fishing journals, and outdoor writers in an ambitious tag-and-release program for yellowfin and bigeye tuna. This alliance has volunteered over $50,000 worth of prizes, incentives, and awards to anglers who tag and release yellowfin or bigeye tuna taken on rod and reel between 1 March and 1 December 1988.

The tags, which are being distributed through leading saltwater tackle stores that serve tuna fishermen, have been provided through the NMFS Cooperative Game Fish Tagging Program, with the costs underwritten by the tackle manufacturers. Named "Tag A Tuna For Tomorrow," this is an excellent example of government, industry, and the angling public cooperating to promote conservation of an important fishery resource.

Midwest Sends Less Nitrogen to Northeast Than Earlier Believed

The Midwest produces much less of the acidic nitrogen falling on the northeastern United States and Canada than is commonly believed, a computer simulation conducted by the Commerce Department's National Oceanic and Atmospheric Administration (NOAA) shows. More than half of the estimated 1.4 million tons of the material deposited annually in the Northeast comes from sources within the region, the simulation of the transport and deposition of acidic nitrogen concluded. It was conducted in two parts by Hiram Levy II and Walter J. Moxim of NOAA's Geophysical Fluid Dynamics Laboratory in Princeton, N.J.

The first portion of the study showed that 25-30 percent of known nitrogen emissions from auto exhausts and smokestacks in the United States are deposited on North America in rain and snow, as "acid rain," and between 25 and 50 percent in dry fall-out. Government monitoring networks support this finding, indicating that approximately half of the total acidic nitrogen falling on the United States and Canada comes from dry deposits.

In a second series of simulations, Levy and Moxim eliminated from the computer model all emissions of nitrogen oxides from sources outside of the northeastern U.S. and eastern Canada. They then compared the resulting wet and dry deposits in the Northeast with the earlier model. This revealed that about two-thirds of the nitrogen oxides deposited in the Northeast in precipitation came from outside the region, while 80 percent of the nitrogen oxides deposited through dry fall-out and about half the total acidic deposits falling on the northeast were emitted from sources within the region.

Based on the model results, the NOAA investigators, in a paper published in *Nature*, concluded that current monitoring in the northeastern United States and Canada exaggerates the role of acid nitrogen transport from the Midwest, Southeast, and the Ohio Valley, and underestimates the importance of local and regional emissions. The project also showed that emissions remaining in the atmosphere, after both wet and dry deposition, are carried off the continent, principally over the North Atlantic. The model indicates that no more than 200,000 tons of acidic nitrogen from North America reach Europe annually—less than 3 percent of the estimated European emissions of nitrogen oxides.

New Data Center Helps Assess Global Climate

The University of Delaware and the National Oceanic and Atmospheric Administration (NOAA) has announced the creation of a new Joint Center for Research in the Management of Oceanographic Data to be headquartered at Lewes, Delaware. "This cooperative endeavor will help discover the answers to global climate change and related regional oceanographic problems, such as sea level rise, along the east coast," according to Thomas N. Pyke, Jr., NOAA Assistant Administrator for Satellite and Information Services.

The new center has been established at the University's College of Marine Studies at Lewes as a clearinghouse for oceanographic data. It will manage the enormous amounts of oceanographic data available for U.S. east coast areas. The center, dedicated 5 May, will process data generated from NOAA's environmental satellites, which keep a watchful eye on many of the oceans characteristics, including surface temperature and the currents that transport pollutants along the coast.

Recent Trends in World Fish Harvests

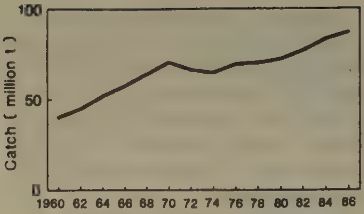

Figure 1.—World fisheries catch, 1960-86.

Table 1.—Annual world fish catch increases, 1980-86.

Year	Catch (million metric tons)	Percent increase
1980	72.1	1.4
1981	74.9	3.9
1982	76.8	2.5
1983	77.3	0.6
1984	83.4	7.9
1985	85.5	2.5
1986	89.6	4.8
Average		3.4

Source: FAO "Yearbook of Fishery statistics."

The world catch of fish, shellfish, and other aquatic organisms reached an all-time record of nearly 90 million metric tons (t) in 1986, according to a preliminary estimate prepared by the Food and Agriculture Organization (FAO) of the United Nations (UN). The estimated 1986 catch was a 5 percent increase over the previous record catch of 85.5 million t set in 1986.[1,2] Despite warnings from environmentalists concerned with rising levels of pollution, fishermen, are continuing to report increasing fishery catches. Since 1980, the world fisheries catch has increased an impressive 25 percent. Developing countries are responsible for most of the increased catch.

Preliminary data suggest that efforts by developing countries in the southern hemisphere to expand their fishing industries will result in continued increases through the year 2000, although this could be affected by a wide variety of economic and climatic factors. The 1986 increase was primarily due to the expanded Asian and, to a lesser extent, Latin American catches. Nearly 40 percent of the total world catch is taken by Asian countries, including Japan, which dominate the world fishing industry. The most rapidly growing catch, however, is in Latin America, where fishery catches have increased by 60 percent since 1980.

Catch Increases

The world fisheries catch has grown steadily since 1980. Annual increases have ranged from a high of 7.9 percent in 1984 to a low of 0.6 percent in 1983 (Table 1). The small 1983 increase was primarily caused by the effects of both the 1982-83 El Niño event in the Eastern Pacific and sharp price increases for fuel. Some observers suggested that the world fisheries catch was leveling off at about 70 million tons in the early 1970's (Fig. 1). The collapse of the Peruvian anchovy fishery in 1971-72 did cause overall world catches to decline during the early 1970's. The predictions, however, that the world catch had reached its maximum potential of conventional species proved erroneous. The expected leveling off did not materialize, and the world catch has expanded continuously since 1977.

The average annual increase during the 1980's was 3.3 percent. The catch since the 1982-83 El Niño has been well above that average level, suggesting that the expansion of the world catch has not yet begun to level off. The increases since 1982 have come mostly from developing countries, and have been achieved even though many countries, especially in Latin America, have had to scale back government-financed fishery development programs as a result of the world debt crisis. Many developing countries have benefited from commercial joint venture arrangements with distant-water fishing companies which in many cases have limited opportunities in their local fisheries and, as a result, have maintained their involvement in overseas fisheries.

The NMFS Branch of Foreign Fisheries Analysis has prepared this article based on the quantity of fish and shellfish harvested. Some of the conclusions based on catch trends would be radically different if the value of the catch was calculated. The Branch, however, has decided to deal only with the quantities involved.

This decision is based on several factors. First, the collection and assessment of value data is a much more difficult undertaking, and would require a research effort that cannot at this time be justified. Second, value data includes many nonfishery components such as prices, interest rates, and exchange rates. As a result, such a study would often show fluctuations because of a number of economic factors other than developments in the fishing industry.

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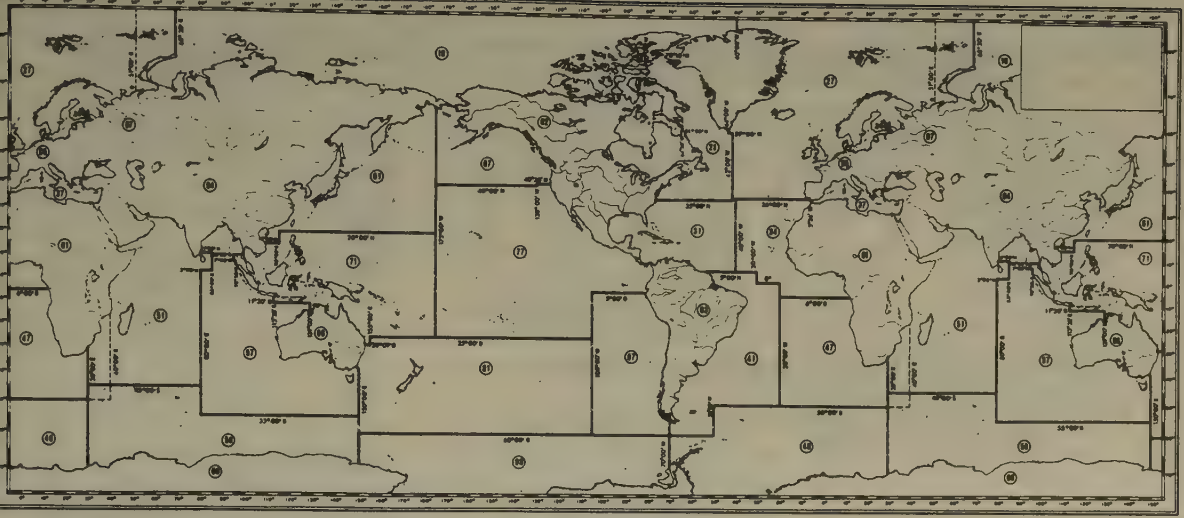
[1] This report was prepared as a combined effort of the NMFS Branch of Foreign Fisheries Analysis. Dennis Weidner coordinated the project and was responsible for the world trend and Latin American sections. Other contributors included: Milan Kravanja (Soviet and Eastern European sections), Paul Niemeier (Asian, Oceanian, Japanese, and Chinese sections), William Folsom and Michelle Miller (Western Euopean section), Melissa Zajk (Canadian section), and Steve Wilkshire (African section). It is based on preliminary FAO data available in mid 1987. More recent FAO estimates suggest that the 1986 catch may have hit nearly 91.5 million tons.

[2] For the purpose of this study, the Branch had adopted the widely accepted FAO statistical conventions. Catch data is attributed to the flag of the fishing vessels harvesting the fish and not by the national coastal zone in which it was harvested. Thus, Soviet catches off the coast of Angola are considered Soviet and not Angolan catches. The primary source used for these statistics is the FAO, which in turn relies on each individual country to supply national data. The year 1980 was selected as the base year to focus this report on recent catch developments and to limit the amount of statistical data assessed. As appropriate, the authors have referred back beyond 1980 to explain important longer-term trends.



Major FAO fishing areas.

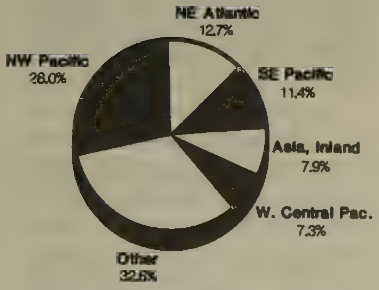


Figure 2.—World fisheries catch by fishing area, 1985.

Table 2.—World fisheries catch, by principal fishing areas, 1985-86.

Region	FAO fishing area	Catch (10⁶ t) 1985	Catch (10⁶ t) 1986	1986 Percentage
Northwest Pacific	61	23.8	24.1	27
Northeast Atlantic	27	10.9	10.8	12
Southeast Pacific	87	9.7	11.9	13
Asia, Inland	04	7.1	7.1	8
W. Cent. Pacific	71	6.2	6.5	7
Others		27.7	29.2	33
Total		84.9[1]	89.6	100

[1] This world 1985 catch figure has been updated by FAO to 85.5 million t (Table 1). The updated figure, however, was not used here as the revised breakdown by FAO area was not yet available.

Table 3.—World fisheries catch by major species, 1985-86.

Species	Catch (10⁶ t) 1985	Catch (10⁶ t) 1986	1986 Percentage
Alaska pollock	6.1	6.6	7
Peruvian anchovy	1.0	5.1	6
Japanese sardine	4.7	4.8[1]	5
South American sardine	5.8	4.3	5
Capelin	2.3	2.2	2
Atlantic cod	1.9	1.9	2
Chilean jack mackerel	2.1	1.8	2
Chub mackerel	1.8	1.8	2
Atlantic herring	1.4	1.4	2
Other	57.8	57.0	
Totals	84.9[2]	89.6	

[1] Estimated

[2] This catch figure, published in the FAO "Yearbook of Fisheries Statistics," 1985, has been updated by the FAO to 85.5 million t (Table 1). The updated figure, however, was not used here as the revised breakdown by FAO species group was not yet available.

For these and other reasons the authors have decided to focus this discussion primarily on catch trends. Readers should, however, be aware of the limitations of the data and conclusions presented in this report.

Fishing Areas

The world fisheries catch comes from three main geographic areas (Fig. 2). The two most important areas are located in the northern hemisphere: the Northwest Pacific, FAO area 61, and the North Atlantic, FAO area 27 (see map). Fishermen took about 34.6 million t of fish and shellfish from these two areas during 1985, over 40 percent of the world total and over 45 percent of total marine catch (Table 2)[3]. Both areas have large continental shelves supporting important fishery stocks, but their domination of world fisheries is also due to the fact that most of the major developed fishing countries (Japan, the U.S.S.R., China, the United States, South Korea (ROK), Norway, Denmark, Iceland, and Canada) are located in the two regions. The third major fishing area is the Southeast Pacific (FAO area 87), where coastal upwelling supports the massive fisheries for small pelagics off of Chile and Peru.

Species of Fish

Only about eight species are caught in quantities exceeding 1.0 million tons annually (Table 3). The world's single largest fishery in terms of quantity is Alaska pollock, *Theragra chalcogram-*

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[3] The 1986 catch by area was not available when this article was written, but the basic pattern is unlikely to change significantly. The FAO data on which this article is based is catch data recorded by the flag of the vessel which caught it and can differ substantially from the area where it is eventually landed.

Table 4.—World catch by major FAO species group, 1980-86.

Name	FAO species group no.	Catch (10^6 t) 1980	1981	1982	1983	1984	1985	1986[1]
Small pelagics	35	15.5	17.0	17.9	17.6	19.7	21.2	
Cods	32	10.8	10.7	11.0	11.2	12.3	12.4	
Jacks/mullets	34	7.3	8.0	7.8	8.0	8.5	8.0	
Misc. freshwater[2]	13	5.2	5.5	5.7	6.2	6.5	7.2	
Redfishes	33	5.4	5.3	5.4	5.0	5.5	5.3	
Mackerel/snooks	37	4.6	4.0	3.8	3.7	4.3	3.7	
Tunas	36	2.6	2.7	2.8	2.9	3.1	3.2	
Shrimp	45	1.7	1.6	1.7	1.8	1.8	1.9	
Others, combined		19.0	20.0	20.7	20.9	21.4	22.0	
Total[3]		72.1	74.8	76.8	77.3	83.1[4]	84.9[4]	89.6

[1] Species group data not available.

[2] Does not include other freshwater species groups: Carps (group 11), tilapias (12), and sturgeons (21); the combined total of these three groups in 1985 was 1.3 million t.

[3] Totals may not agree due to rounding.

[4] These world 1984 and 1986 catch totals have been updated to 83.4 million t and 85.5 million t, respectively in Table 6, but are not to be used here as the revised breakdown by FAO species group was not available.

Table 5.—World catch increase of major species groups, 1980-85.

Name	FAO species group	Changes 1980-85 Amt. (10^6 t)	Percent
Small pelagics	35	5.7	45
Other (unspecified)		3.0	23
Misc. freshwater	13	2.0	16
Cods	32	1.6	12
Jacks/mullets	34	0.7	5
Tunas	36	0.6	5
Shrimps	45	0.2	2
Redfishes	33	−0.1	−1
Mackerels/snooks	37	−0.9	−7
Total		12.8	18

ma, and reported catches of that species totaled 6.6 million t in 1986. Most of the fisheries for these important species were little changed in 1986. The only major shift was a massive increase in the Peruvian anchovy fishery. Fishermen from Peru and Chile reported a 1986 catch of 5.1 million t, more than a 400 percent increase from the 1.0 million t reported in 1985.

North Pacific pollock fishermen reported the only other significant increase (+0.5 million t). Peruvian and Chilean fishermen reported the largest declines, in the sardine (−1.5 million t) and jack mackerel (−0.3 million t) fisheries.

The world catch is composed primarily of three species groups: Small pelagics, cods, and jacks, which had a combined catch of over 40 percent of the world catch for all species in 1985 (Table 4). The single most important group is small pelagics (anchovies, herrings, sardines, etc.) and catches of that group totaled 21.2 million t, nearly 25 percent of the world total for all species. About half of the increase in the world catch since 1980 has resulted from increased catches of these small pelagic species (Table 5). Other important increases were reported for various other marine fish and shellfish (up 23 percent), miscellaneous freshwater fish (up 16 percent), and cods (up 13 percent).

The massive increases of small pelagics is significant because the expansion of these fisheries means that the increase of the world catch has not resulted in a corresponding increase in the production of edible commodities. A large portion of the small pelagic catch is reduced to fishmeal, used principally for animal feed[4]. Catches of all major species groups used for edible products have been increasing at very low rates or have actually declined (Table 5)[5]. It should also be noted that small pelagic fisheries are subject to sharp annual fluctuations. Overall fluctuations may be less likely in the 1980's as fishing effort is now divided over a number of different stocks. In the early 1970's, small pelagic fisheries were centered on a single species, the Peruvian anchovy. The catch of Peruvian anchovy in 1970 was 13.1 million t, 60 percent of the world small pelagic catch of 21.4 million t. Obviously, significant changes in that stock had a major impact on the total world catch of small pelagic species. Catches are now more widely diversified over several different stocks in different areas. The most important small pelagic taken in 1985 was South American sardine, but its catch of 5.8 million t was only 27 percent of the 21.2 million t of small pelagics taken worldwide. Various small pelagic species react differently to climatic changes. Thus, while Peruvian anchovy declined after the 1972 El Niño, stocks of sardine and mackerel increased. Thus, when stocks are more diversified, fluctuations of one species may, to some extent, be offset by countervailing fluctuations of other species.

Developed and Developing Countries

A major shift occurred in the harvest of world fishery resources during the 1980's. Developing countries replaced developed countries as the principal world harvesters of fishery stocks (Fig. 3)[6]. The developed countries have traditionally dominated world fisheries. In 1980, developed countries reported a catch of 38.4 million t, or 53 percent of the world total (Table 6). Since 1980, the developed countries have reported only a modest catch increase of 12 percent to 42.9 million t in 1986. The combined effect of overfishing in the coastal waters of developed countries (primarily in the North Atlantic and North Pacific) and the increasing restrictions, placed by developing countries on distant-water fishermen have limited the recent catch

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[4] Eventually, of course, most of the animals are slaughtered for human consumption. so even fishmeal production does increase food production. The increase of poultry and livestock produced, however, will only be a fraction of the amount of fish used to produce the fishmeal.

[5] Cods are the only major species group used primarily for direct human consumption that has increased more than 5 percent since 1980.

[6] The FAO's definition of developed and developing countries is used. The FAO breakdown is detailed in Table A-5 of the 1985 "Yearbook of Fishery Statistics." Data submitted by some developing countries should be considered rough estimates as they are often computed without an extensive data collection system.

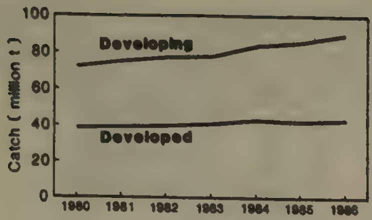

Figure 3.—Fisheries catch by type of country, 1980-86.

Table 6.—World fisheries catch, by type of economy[1], 1980-86.

	Catch (10⁶ t)		
Year	Developed	Underdeveloped	Total
1980	38.4	33.8	72.1
1981	39.0	35.8	74.9
1982	39.4	37.4	76.8
1983	40.4	36.9	77.3
1984	42.7	40.7	83.4
1985	41.9	43.6	85.5
1986	42.9	46.7	89.6

[1] Developed and developing countries are identified in Table A5 of the 1986 edition of the FAO "Yearbook of Fishery Statistics."

Table 7.—Catch and industry data for major fishing countries, 1986.

	Catch		
Country	Amt. (10⁶ t)	Share[1]	Type of industry
Japan	11.9	13%	Private
U.S.S.R.	11.1	12	State owned
China	7.3	8	State owned
Chile	5.6	6	Private
Peru	5.3	6	Mixed
United States	4.9	5	Private
Korea (ROK)	3.1	3	Private
India	2.8	3	Private
Indonesia	2.5	3	Private
Thailand	2.1	2	Private
Norway	1.9	2	Private
Philippines	1.9	2	Private
Denmark	1.8	2	Private
Korea (DPRK)	1.7	2	State owned
Iceland	1.6	2	Private
Canada	1.5	2	Private
Other	22.6	25	
Total	89.6		

[1] Percentage of the total world catch.

Table 8.—World fisheries catch of major fishing countries by economic organization, 1986.

Type of industry	Catch[1] (10⁶ t)	Percentage
Private	41.6	62
State owned	20.1	30
Mixed	5.3	8
Total	67.0	100

[1] Only the catch of the major fishing countries detailed in Table 9 are computed in this table. These countries represent about 75 percent of the world catch.

increases of the developed countries. Developing countries, on the other hand, achieved a catch of 46.7 million t by 1986, or 52 percent of the world total. The 1986 catch of the developing countries was nearly 40 percent over 1980 levels. (From 1967 to 1971 the total catch of the developing countries increased sharply because of massive catches of Peruvian anchovy.) The steadily expanding catch of Chile and Peru and the rapidly expanding fisheries of several developing Asian countries account for most of the increase. Many developing countries, however, have not participated in this expansion. Few African countries, for example, have increased their catch since 1980, even though fish is a critical component of the diet in many of them.

Type of Industry

The economic organization of the major fishing countries varies sharply (Table 7). The two leading countries are classic examples of private (Japan) and state-owned (Soviet Union) fishing industries. Japan's fishing industry is the most modern in the world, efficiently providing food and jobs to Japan as well as tax revenues to the Government. In recent years, however, the Government has increasingly funded programs to assist Japanese fishermen adjusting to the ever tightening restrictions on distant-water fishing. The Soviet fishing industry, only slightly less productive than the Japanese, is markedly less efficient.

A rough estimate of the relative efficiencies of the two countries can be obtained by comparing their fleets. The Soviets, in 1986, reported a fleet of 2,800 fishing vessels totaling 3.7 million gross tons. The Japanese, on the other hand, exceeded the Soviet catch with a much smaller fleet, about 2,700 vessels totaling only 0.9 million gross tons. Precise data are not available on the profitability of the Soviet fishing industry, but it is widely believed that the real cost of the fish produced by the Soviets could not be justified by market-based prices. (An accurate comparison of the two countries would require a much more detailed assessment including differences in fleet deployment, target species, operating costs, markets served, and many other factors.)

The predominant pattern for fishing industries is private companies. Of the 16 leading countries in 1986, 11 with over 60 percent of the world catch had basically privately owned industries (Tables 7, 8). Three countries with 30 percent of the catch had state-owned industries. Only one major fishing country (Peru) had a mixed fisheries economy with ownership by both private and state-owned companies.

Pollution

Environmentalists warn that increasing levels of pollution may adversely affect fisheries production. The United Nations Environmental Program (UNEP) has attempted to address the oceanic pollution problem through its Regional Seas Program, but most observers continue to report rising levels of pollution in the world's oceans. Some small fisheries have been impaired, especially freshwater fisheries and estuarine-dependent coastal fisheries. Marine debris, especially "persistent" plastic materials, is causing increasing mortalities of several marine mammals, sea turtles, birds, and other marine life. Environmentalists, however, have not yet compiled conclusive evidence to substantiate their concerns regarding damage to the major marine fish stocks such as Alaska pollock, capelin, Japanese or Chilean sardine (FAO refers to some sardines as pilchards), or others as a result of marine pollution.

The world fisheries catch has expanded during the 1970's and 1980's despite increasing levels of pollution. Increases have been reported even in heavily polluted areas. For example, the Mediterranean is probably the FAO area most heavily polluted, but catches there increased from 1.6 million t in 1980 to 1.9 million t in 1985. Some observers warn that pollution is affecting fish stocks, but the impact, if any, has so far been masked by other factors. Fish stock abundance has apparently been affected less profoundly by pollution than the combined effects of increasing fishing effort and climatic variations. The effects of these two variables may be masking the more limited impact of pollution on important marine stocks. Considerable caution should be used in using global catch statistics to assess the impact of pollution. Most of the increased fisheries catch since 1980 has come from a small number of small pelagic stocks (Table 5). A thorough examination of the pollution problem would have to assess possible impact on the much larger number of traditional species for which catches have increased only marginally despite substantially increased fishing effort (Table 5).

While scientists have yet to prove that substantial declines in catches of major marine species have been caused by pollution, there is mounting evidence that some marine stocks are being affected. While the catch of cods as a group has increased since 1980 (Table 4), scientists are increasingly concerned over Atlantic cod (Table 3). Atlantic cod catches have declined from 2.2 million t in 1980 to only 1.9 million t in 1985.

Pollution does result in the contamination of some fishery resources. However, concerns over product safety are for the most part limited to freshwater fish and marine or near-coastal species subject to incidental exposure to industrial and agricultural chemicals such as PCB's and pesticides. It should be noted also that many of the species likely to be affected are caught by recreational fishermen and may not be of major commercial importance. Individual countries vary in the extent to which they are alert to these problems. Some countries provide effective consumer protection through the issuance of public health advisories and, if judged necessary, by closure of selected fisheries. Action levels for specific contaminants are set with the added insurance of large safety factors, usually several orders of magnitude.

Table 9.—World fisheries catch by regions, 1980-86.

Region	Catch (10^6 t) 1980	1981	1982	1983	1984	1985	1986	Percent increase 1980-86
Asia	30.1	31.5	32.3	34.0	36.0	36.7	38.2	27
Latin America	9.6	10.3	11.4	9.2	12.0	13.6	15.6	62
Europe	12.5	12.5	12.2	12.6	12.9	12.6	12.3	−2
U.S.S.R.	9.5	9.6	10.0	9.8	10.6	10.5	11.1	17
North America	5.1	5.3	5.5	5.7	6.2	6.3	6.6	29
Africa	4.1	4.3	4.1	4.4	4.1	4.1	4.2	2
Middle East	0.8	0.9	0.9	1.0	1.0	1.0	1.0	25
Oceania	0.5	0.5	0.5	0.6	0.6	0.6	0.6	20
Total[1]	72.1	74.9	76.8	77.3	83.4	85.5	89.6	24

[1]Totals may not agree because of rounding.

Table 9a.—World fisheries catch increase, 1980-86.

Region	Percent increase (1980-86)	Region	Percent increase (1980-86)
Latin America	62	U.S.S.R.	17
North America	29	Africa	2
Asia	27	Europe	−2
Middle East	25		—
Oceania	20	World average	24

Geographic Regions

The world fisheries catch is dominated by Asian[7] fisheries (Table 9). Asian fishermen caught 38.2 million t of fish and shellfish in 1986, nearly 40 percent of the total world catch (Fig. 4). The most rapidly growing area, however, is Latin America, and catches in that region, especially in the Pacific, have grown over 60 percent since 1980 (Table 9a), primarily because of steadily increasing catches of small pelagic species by Chile, Peru, and Ecuador. Major developments in each of the important world fishing regions are given below.

Asia

Asian countries dominate the world fishing industry, accounting for over 40 percent of the total world catch in 1986 (Table 9). The Asian catch increased by 4 percent over the 1985 catch and has increased by over 25 percent since 1980. One of the most significant developments in Asia during the 1980's has been the steady increase of important aquaculture industries. At first, farmers in developing countries targeted low-valued species for local consumption, but many others increased the production of high-valued species for luxury markets. The most spectacular development has been the massive expansion of the pond-shrimp industry. The Branch estimates that Asian shrimp farmers harvested about 260,000 t of shrimp in 1986, nearly a 400 percent increase from the 55,000 t harvested as recently as 1982. The leading shrimp farming countries

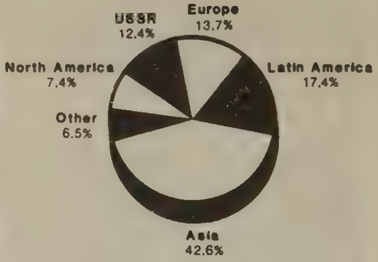

Figure 4.—World fisheries catch by region, 1986; total for 1986 was 89.6 million t.

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[7] The Branch has chosen to assess fishery catch developments by continent because of interest in national developments. Such an analysis, however, is not a good way of organizing biological trends, especially for regions such as Asia and Latin America which have coasts spanning two or more oceans. An assessment by ocean region could provide useful insights, but for the purposes of this study this subject has been addressed only briefly. Note also that the following data is calculated on the basis of the flag of the fishing vessel, and not where the fish was caught. In some regions, especially Africa, the regional catch total would be much higher if the catch of the distant-water countries operating off Africa was added to the regional total.

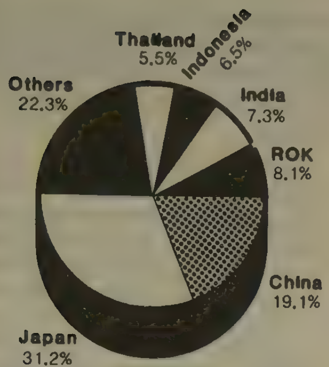

Figure 5.—Asian fisheries catch by country, 1986; total for 1986 was 38.2 million t.

are China, Taiwan, Indonesia, the Philippines, and India.

Japan is the single most important Asian fishing country, but the region's catch is divided among seven other major countries: China, South Korea (ROK), India, Indonesia, Thailand, the Philippines, and North Korea (DPRK) (Fig. 5). Eight of the world's 16 leading fishing countries are Asian (Table 7). These eight countries accounted for 87 percent of the 1986 regional catch. All of these countries, except for Thailand and the Philippines, reported catch increases in 1986. The fishing industry plays a much more important economic role in these countries than is the case for the United States or European countries. In Japan, for example, about half of the animal protein consumed is derived from marine organisms.

Asian countries reported several major developments in 1986. Japan harvested a near record 11.9 million t and reported increased aquaculture production and offshore catches, especially of sardines. China reported steady growth in all sectors of the fishing industry. The 7.9 million t catch increased 7 percent and included impressive increases in marine and freshwater fisheries and aquaculture. Chinese Government officials are projecting a catch of 9 million t by 1990, primarily as the result of increased aquaculture production. The ROK 1986 catch totaled 3.1 million t, an impressive 15 percent increase over 1985 results. Much of the ROK increase was due to the country's expanding U.S. joint venture fishery and entry into the squid fisheries of the North Pacific and Southwest Atlantic. The country's aquaculture industry has also continued to grow steadily.

India's catch of 2.8 million t has changed little since 1984, with most of the marine catch coming from heavily exploited inshore waters. The Indian Government has been trying to promote a deep-sea fishery since 1968, but has had only limited success. Indonesia reported a 1986 catch of 2.5 million t, an increase of 9 percent over the 1985 catch. Indonesia, like India, depends on artisanal fishermen using traditional methods for most of its catch. The 1986 increase was primarily due to the gradual mechanization of the Indonesia fleet, extending its range to more distant coastal fishing grounds. Government officials believe that the country can significantly expand the fisheries catch to as much as 8 million tons.

Thailand and the Philippines both experienced slight declines in 1986. Thai grounds are heavily fished and Thai fishermen are having increasing difficulty maintaining their fisheries off other countries. Filipino fishermen have some of the same problems and may be feeling the effect of using such destructive fishing practices as using dynamite and cyanide. Much of the decline in the Filipino catch is being offset by the steady growth in the country's aquaculture industry.

Latin America

Latin American countries report the world's second most important fisheries catch, representing nearly 20 percent of the world total. Over 80 percent of the Latin American catch is taken in the Pacific. Catches totaled 15.6 million t in 1986, a 15 percent increase over the 13.6 million t taken in 1985. The 15.5 million t total does not include the more than 1.0 million t taken by distant-water countries (primarily the U.S.S.R., Poland, and Japan) off various Latin American countries (primarily Argentina, Chile, and Peru). Latin American catches increased in 1986 to a level approaching the record regional catch levels taken before the collapse of the Peruvian anchovy fishery in 1972.

Two countries, Peru and Chile, dominate Latin American fisheries (Fig. 6). Chile is the leading country with a catch

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The Taiwanese Fishing Industry

Taiwan's 1986 fisheries catch totaled a record 1,095,000 t, nearly a 6 percent increase over the 1985 catch of 1,038,000 t. The value of the 1986 catch increased even more (by over 18 percent) to almost $2 billion. The deep-sea fisheries catch, over 45 percent of the total, was nearly 500,000 t. Inshore, coastal, and aquacultural production totaled 276,000 t, 55,000 t, and 266,000 t, respectively.

Taiwan exported 265,000 t of seafood in 1986, valued at $1.2 billion, an increase of 19 percent by quantity and 43 percent by value over 1985 exports. (The large increase in value reflects, in part, the fact that the new Taiwan dollar appreciated by 13 percent against the U.S. dollar in 1986.) Shrimp, eel, and tuna continued to be the three major fishery export commodities, comprising a combined 43 percent by quantity and 76 percent by value of total 1986 fishery exports. Japan was by far the largest purchaser of Taiwan's fishery products, followed by the United States, Australia, Saudi Arabia, Hong Kong, Italy, and the Federal Republic of Germany. The American Institute in Taiwan has prepared a 28-page report on Taiwan's fishing industry in 1986-87 containing a general outline and sections on the fisheries catch, fleet, processing capability, development plans, trade, and international agreements. The report also includes a brief section describing opportunities for U.S. exporters of fishery products and equipment. U.S. companies can obtain a copy of this report for $12.95 plus a $3.00 handling fee (personal check or money order) by ordering report number PB88-209002/GBA from the National Technical Information Service, U.S. Department of Commerce, Springfield, VA 22161.

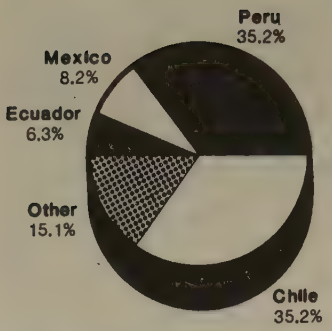

Figure 6.—Latin American fisheries catch by country, 1986; total for 1986 was 15.6 million t.

totaling 5.6 million t in 1986, followed by Peru with a catch of 5.3 million tons. The two countries combined accounted for 70 percent of the regional total. Almost all of the Latin American 1986 increase was the result of increased harvests by these two countries. Over 90 percent of the Chilean and Peruvian catch is sardine, anchovy, jack mackerel, and horse mackerel which is reduced to fishmeal. Peru reported substantially increased anchovy catches in 1986. Anchovy was the mainstay of the Peruvian fishing industry during the 1960's and early 1970's, but had declined to negligible levels in 1985. The Chilean increase was also due to increased anchovy catches, as the sardine and jack mackerel declined. Other important fishing countries in the region include: Mexico (1.3 million t), Ecuador (1.0 million t), Brazil (0.9 million t), and Argentina (0.4 million tons).

A few species dominate the Latin American catch. Latin American countries primarily harvested massive quantities of the reduction species mentioned above. Fishermen also conduct smaller fisheries, but in some cases more valuable ones, for hake, tuna, shrimp, and lobster. A wide variety of other species are caught in smaller quantities.

Several countries reported major fishery developments in 1986. Mexico significantly expanded its tuna industry, and now operates one of the world's most modern tuna fisheries. Ecuador reported record results in its pond shrimp industry which allowed it to become the second most important source of shrimp imported by the United States. Many observers believe that Ecuador may replace Mexico as the major source of U.S. imported shrimp in 1987.

Argentina achieved encouraging results because of a strengthening international market for groundfish, the country's principal fishery, but fishermen reported a declining shrimp catch. Argentine companies complained of increasing competition with the foreign companies operating off the Falklands. The British announced in 1986 that they planned to begin managing fishery resources off the Falklands. Chilean farmers have begun to harvest salmon; while harvests are still small, some observers believe it could develop into an important new fishery. Peru reported a sharp drop in its new scallop fishery, but Panama reported an increase. At the end of 1986, several Eastern Pacific countries began to report a mild El Niño event, but it apparently had little impact on year-end results. The event was centered in waters off Ecuador and northern Peru. Preliminary reports suggested that the 1987 catch of several countries might have been significantly affected.

Europe

European fishermen caught 12.3 million t of fish and shellfish in 1986, making Western Europe the third most important fishing area in the world. European catches, unlike those of many other regions, have remained stable during the past 7 years, ranging from a low of 12.2 million t in 1982 to a high of 12.9 million t in 1984. The major fishing countries are the Scandinavian countries and Spain (Fig. 7).

Eastern Europe

Eastern European countries harvested almost 1.4 million t of fish and shellfish in 1986, or over 35 percent more than in 1970 when the total catch amounted to only 1.0 million tons (Table 10). The most important country is Poland, which harvested 0.6 million t, nearly half of the total for the entire region. The Poles consume about 17 kg per capita of fishery products annually,

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Peruvian Fisheries, 1986-87

Peru's 1986 fisheries catch totaled 5.5 million t, a 34 percent increase over the 1985 catch, mostly generated by a 300 percent increase in the anchovy catch. The catch of other major species declined. Fishery exports in 1986 were 780,000 t, an increase of 13 percent, mostly because of increased fish meal production. Fish meal exports accounted for about 8 percent ($200 million) of Peru's total 1986 export earnings. The Peruvian Government, in early 1987, initiated a Fisheries Reactivation Fund aimed at rebuilding the fleet and upgrading the equipment of the artisanal fishermen. The Fund will be financed by a 5 percent tax on the fishmeal exports earnings of the private companies.

The Government plans to increase nontraditional exports, including frozen shrimp and scallops, by making credit available and improving the management of these resources. The Peruvian Government is also promoting domestic consumption of fishery products by creating a state-owned fishing fleet (FLOPESCA) and negotiating joint venture agreements with distantwater-fishing countries. The U.S. Embassy in Lima has prepared an 18-page report reviewing the status of the Peruvian fishing industry in 1986 and 1987. The report covers the 1986 fisheries catch, impact of the fishing industry on the economy, state-owned companies, domestic consumption, modernization of the fleet, fishmeal production, new initiatives (shrimp and scallops), joint ventures (Cuba and the U.S.S.R.), 1987 projections, and implications for U.S. exporters. The report includes statistical tables, with data available up to June 1987. U.S. companies can obtain a copy of the report "Peru: Annual Fisheries Report, 1986-87" for $12.95 and a $3.00 handling fee (total $15.95, personal checks or money orders only) by ordering report PB88-205422/GBA from NTIS, Springfield, VA 22161.

the highest in Eastern Europe. Most of the Polish catch is taken by the country's distant-water fleet which extended its operations in the southern Atlantic. The Poles currently conduct a major fishery for squid and southern blue whiting off the Falklands.

Bulgaria, East Germany (GDR), and Romania also obtain most of their fisheries catch from distant-water operations. Most of the Eastern European catches peaked in 1975 before the extention of 200-mile zones by many coastal countries. The major exception is Romania, whose catch has more than doubled since 1975. Yugoslavia and Albania, unlike the other Eastern European countries with marine coasts, fish primarily in coastal Adriatic waters. Both countries report only small catches. The isolationist tendency of Albania has discouraged the development of a fishing industry. Landlocked Hungary and Czechoslavakia harvest a

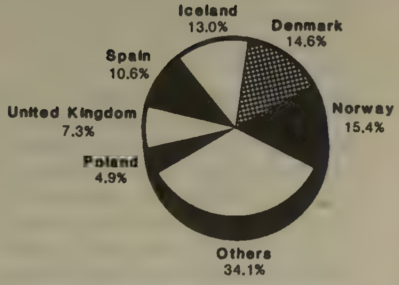

Figure 7.—European fisheries catch by country, 1986; total for 1986 was 12.3 million t.

Table 10.—Eastern European fisheries catch, 1970-86.

Country	Catch (10^3 t) 1970	1975	1980	1985	1986	Population in millions (1986)	Consumption (kg per capita)
Poland	469.3	800.7	640.6	693.5	645.2	37.2	17.3
Romania	58.6	136.6	173.6	237.6	271.1	22.7	11.9
E. Germany (GDR)	321.6	376.2	236.3	197.7	208.9	16.7	12.5
Bulgaria	95.6	158.1	126.4	100.2	109.2	9.0	12.1
Yugoslavia	46.2	56.6	56.4	75.0	77.6	23.1	3.4
Hungary	26.0	30.8	33.7	36.9	36.1	10.6	3.4
Czechoslovakia	13.4	16.9	16.0	19.8	20.7	15.5	1.3
Albania	4.0[1]	4.0[1]	4.0[1]	4.0[1]	4.0[1]	3.1	1.3
Total	1,034.9	1,579.9	1,286.0	1,364.7	1,372.8	137.9	10.0

[1] Estimated

FRG SEAFOOD MARKET, 1986

The demand for fishery products in the Federal Republic of Germany (FRG) has increased from $1.0 billion in 1985 to $1.5 billion in 1986, and could exceed $2.0 billion by by 1990. German per capita consumption of fishery products rose from 11.8 kg in 1985 to 13.2 kg in 1986 because of greater consumption of frozen fish by private households, institutions, and "fast-food" restaurants. In 1986, frozen fish outsold fresh fish for the first time. Purchases of frozen fish products, particularly frozen fish sticks and fish fillets, are expected to continue and to contribute to growth in the German fish consumption.

Landings by the FRG fleet during 1986 decreased to 201,000 t from 229,000 t in 1985. Fishery landings are expected to decline to 185,000 t by 1990 due to the reduction of the fleet, which now consists of 7 fresh fish trawlers and 5 stern factory trawlers. As a result, imports will continue to supply most of the rapidly increasing German demand for fishery products. Fish and seafood imports in 1987 are expected to reach $1.1 billion compared with $0.6 billion in 1985. Imports of fishery products from the United States amounted to only $8 million in 1986. On the other hand, the United States imported $75 million worth of fishery products from the FRG in 1986. The U.S. Consulate General in Hamburg has prepared a 9-page report reviewing the market for fishery products in the FRG. The report includes statistical tables of landings, trade, and consumption, and lists of trade fairs, trade associations, and trade publications. U.S. companies can obtain a copy of "The Federal Republic of Germany's Seafood Market, 1986" for $9.95 and a $3.00 handling fee (total of $12.95, personal checks or money orders only) by ordering report PB88-114582/GBA from NTIS, Springfield, VA 22161.

Fish Consumption Grows in France

French consumption of fresh, frozen, and otherwise processed fish and shellfish during 1984 increased to some 680,000 t, or 11 kg per household. This 4 percent increase continues an upward trend observed since 1979. Sales of frozen seafood increased by 10 percent, while sales of smoked, dried, or salted seafood rose by 4 percent. Of the total fishery market, whole fresh fish represent over half of sales. Particularly important species are whiting, pollock, cod, hake, and sardines. Traditional methods of marketing fish in France (fishmongers, open markets) have given way to dominance by large supermarkets. During 1984, supermarkets handled more than one-fourth of all the whole fresh fish sold in France and 37 percent of the fresh fillets.

Despite steadily decreasing inflation in France since 1982, the average retail price for fish has increased more than 18 percent from 1984 to 1985, due to higher transportation and storage costs. The U.S. Embassy in Paris has prepared a 9-page report reviewing the French market for fishery products during 1984, including data on sales, pricing, and distribution of seafood. U.S. companies can obtain a copy of "The French Fishing Industry, 1984" for $9.95 and a $3.00 handling fee (total $12.95, personal checks or money orders only) by ordering report PB88-114640/GBA from NTIS, Springfield, VA 22161.

small catch from inland waters and growing fish culture operations.

Western Europe

Increases in catches have taken place mostly in Iceland, the Netherlands, and Ireland, while decreasing in Norway, the Federal Republic of Germany, Spain, and Portugal. The decline in the Western European catch was caused by overfishing, stricter enforcement of regulations in the heavily fished European waters, and the loss of traditional distant-water fishing grounds. Of particular concern to many European nations has been the decline in popular species such as Atlantic cod, saithe, and haddock catches in the North Sea. The discovery of rich squid fishing grounds off the Falkland Islands has helped maintain catch levels for the Spanish fleet, which has been particularly hard-hit in recent years. The European Community (EC) is actively seeking new fishery agreements with developing nations around the world which will permit EC vessels to continue fishing.

U.S.S.R.

The U.S.S.R. is the world's second most important fishing country. The Soviets reported a 1986 catch of 11.1 million t, a 6 percent increase from the 10.5 million t reported in 1985. (This does not include the fish taken by U.S. fishermen and then sold over-the-side to the Soviets. These joint venture purchases provided the Soviets an additional 223,000 t in 1986.) The Soviet Union has invested massively in developing its high-seas fisheries for both economic and strategic reasons.

Table 11.—The U.S.S.R. fisheries catch, 1976-86.

Year	Catch (1,000 t)	Change[1]	
		Tonnage	Percentage
1976	10,121	157	1.6
1977	9,351	-770	-7.6
1978	9,000	-351	-3.8
1979	9,049	49	0.5
1980	9,476	427	4.7
1981	9,546	70	0.7
1982	9,957	411	4.3
1983	9,757	411	-0.2
1984	10,593	836	8.6
1985	10,523	70	-0.1
1986	11,100	567	5.4
10-Year change		+979	+9.7

[1] Change from previous years, in 1,000 t and percentage.

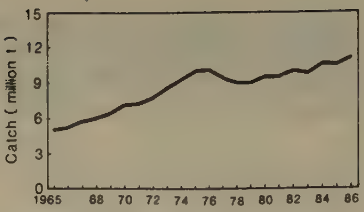

Figure 8.—Soviet Union fisheries catch 1965-86.

From a relatively small catch of about 1 million t in the 1920's, Soviet fishermen expanded their operations into all of the world's oceans and harvested over 11 million t of fishery products in 1986 (Table 11). The Soviets first reached the 10 million t harvest in 1975, before most major coastal countries extended their fisheries jurisdiction to 200 miles (Fig. 8). In the years that followed, many coastal fishing countries severely limited (the United States and Canada) or prohibited (the EC) Soviet fishing operations. Soviet fishermen developed a reputation for ruthless exploitation of fishery resources and many coastal countries extended their coastal jurisdiction to 200 miles to protect their coastal resources from Soviet and other distant-water fishermen. As a result, the Soviet fisheries catch decreased by over 11 percent during 1977-78 and did not reach the 10 million t level again until 1984 (Table 11).

The Soviets were much slower than the Japanese in countering the limiting effects of extended jurisdiction by concluding joint-venture and fisheries-assistance agreements. Their state-owned company, Sovrybflot, though ad-

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Norwegian Salmon Exports

Norwegian fish farmers seem set to break all previous records in farmed salmon exports. Total exports for 1988 could well outstrip last year's figures by as much as US$166 million, according to the Norwegian Information Service, Norinform. Production and exports have soared so far this year, and the final export figure for 1988 will be between US$500 and 590 million.

First quarter sales figures showed a first-hand turnover of US$107 million, compared with US$67 million last year. Production in the same quarter was 15,625 tons, against 11,720 million tons in the same period last year. Information officer Odd Ustad in the central sales organisation for fish farmers says that favorable temperatures have stimulated growth, and that the major disease problems appear to be under control. Demand in the markets is high, with France retaining its first place as recipient of Norway's farm salmon.

Norwegians Target Antarctic's Krill

Three Norwegian firms are planning to harvest the bountiful supplies of krill in the Antarctic to sell to the United States, Great Britain, and Japan, according to the Norwegian Information Service. Millions of dollars will be invested in projects which are scheduled to be under way as early as autumn 1988, when giant factory ships will move south to start the fishing.

The high-protein, shrimplike krill can, according to Norwegian sources, be eaten plain, ground into forcemeat, or served as krill "sticks." It can also be used as a coloring matter for other foods such as trout, salmon, and sausages. Furthermore, krill oil, rich in polyunsaturates, could be useful to the pharmaceutical industry, as a possible rival to cod liver oil, Norinform reports. About 200-250 tons of krill per day is believed a realistic target and the Norwegians believe that there will be no danger of depleting the enormous resources for "many years." However, they also warn that if the supplies of krill, the main food of seabirds and whales, were to be threatened, the entire ecological balance of the oceans could be disrupted.

ministered by capable and experienced managers, was saddled with numerous regulations and bureaucratic inefficiencies that are so prevalent in Soviet operations with foreign companies. This may change now that former Minister of Fisheries (V. M. Kamentsev) was appointed by General Secretary Gorbachev to become not only a member of the Soviet Council of Ministers, but also Chairman of the Federal Foreign Economic Commission. In this latter capacity, Kamentsev will oversee and determine the policy of joint ventures with foreign countries and companies.

One important trend in Soviet fisheries since 1980 has been an increasing reliance on coastal waters. Soviet catches in coastal waters (FAO areas 18, 27, and 61) totaled 6.7 million t in 1985, a 30 percent increase over the 5.1 million t reported in 1980. All of the increase has occurred along the Soviet Pacific coast as catches along the heavily fished Atlantic and Barents Sea coast have declined and catches along its northern Arctic coast are negligible. The Soviets have also shifted their fishing industry from the Atlantic to the Pacific (Fig. 9). Soviet fishery harvests (by FAO fishing area) have changed greatly during the last decade. In 1975, the Soviet Atlantic catch (5.0 million t) was more than twice the Pacific catch (2.2 million t). By 1985, this relationship had totally changed and the Soviet Pacific catch, at 6.2 million t was 50 percent larger than the Atlantic catch of 4.1 million t (Table 12).

The Soviet Atlantic catch has decreased in all regions, except the Southeast Atlantic (FAO area 47) off Namibia and Angola where the Soviets operate under the International Commission for Southeast Atlantic Fisheries (ICSEAF) regulations. In the Northwest Atlantic (FAO area 21), the Soviet catch has declined over 1.0 million t between 1975 and 1985 as the United States and Canada extended their fisheries jurisdiction to 200 miles and severely reduced distant-water fishing. In the Northeast Atlantic (FAO area 27) the Soviet catch has declined another 1.2 million t because of declining stocks and the fishing regulations enforced by the European Community (EC) and several coastal countries. The Soviet fishery in that area is now limited to the Barents Sea and international waters between Iceland and the Svalbard Islands. Worried by a tottering resource base and the Soviet penchant for relentless overfishing, the EC has permitted no Soviet fishing since extending their coastal zone to 200 miles in 1977.

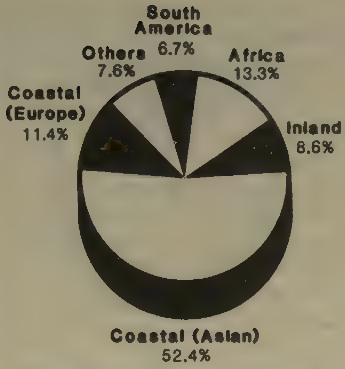

Figure 9.—Soviet Union fisheries catch by area, 1985; total for 1985 was 10.5 million t.

In the Western Central Atlantic (FAO area 31), the Soviet catch has always been small and proved such an economic burden that they abandoned it in 1977. The Soviets, however, retain a vessel repair and transshipment operation in Havana, Cuba. In the Eastern Central Atlantic (FAO area 34), the Soviets conduct one of their most important distant-water operations aided by bilateral agreements with several African countries and by fishing in the coastal waters of several countries with which they have no such agreements. Few African countries have effective surveillance and enforcement capabilities.

In the Pacific, the largest Soviet fishery has historically been conducted off their own coasts and the adjacent waters of the Bering Sea and Northwest Pacific (FAO area 61). The catch in this area has doubled during the past 10 years, but it remains greatly, and possibly dangerously, dependent on a single species, the Alaska pollock. The Soviet pollock catch, amounting to 3.3 million t in 1985, or 30 percent of the entire Soviet catch in that year. It is landed in Siberian ports and then primarily shipped by rail to population centers in the western part of the country where it is marketed to Ryba and other retail stores. Few other Pacific grounds are important to Soviet fishermen, except for the Southeast Pacific where the Soviets fish outside the 200-mile zones of Peru and Chile. Efforts to gain access to coastal waters failed when the Allende Government fell in Chile during 1973 and when the Peruvians refused to renew joint venture agreements in 1985.

In the Antarctic, the Soviets have attempted to initiate a krill fishery, and catches reached a record 0.5 million t in 1982. The operation, however, proved difficult and costly, and Soviets had difficulty marketing krill products. Catches declined sharply in 1983 and in 1985 totaled only 0.2 million tons. The Soviets announced in late 1987 some technical innovations which they believe

Table 12.—U.S.S.R. fisheries catch for selected years by major fishing areas, 1970-85.

Fishing grounds	FAO area	Catch (1,000 t) 1970	1975	1980	1985
Inland waters	7	855	944	753	906
Black Sea	37	303	350	391	345
Atlantic					
Northwest	21	812	1,167	108	133
Northeast	27	1,566	2,406	1,984	1,239
W. Central	31		69		
E. Central	34	613	1,166	942	708
Southwest	41	421	9	28	71
Southeast	47	423	421	825	698
Subtotal		4,993	6,532	5,031	4,100
Indian Ocean					
Western	51			37	32
Eastern	57				1
Subtotal				37	33
Pacific					
Northwest	61	1,448	2,719	3,196	5,462
Northeast	67	748	573	59	11
W. Central	71			4	10
E. Central	77	20	31		1
Southwest	81		45	70	66
Southeast	87			552	624
Subtotal		2,216	3,368	3,881	6,174
Antarctic					
Atlantic	48			424	188
Indian Ocean	58			103	28
Pacific	88				
Subtotal				527	216
Grand total		7,209	9,900	9,476	10,523

Source: FAO "Yearbook of Fishery Statistics," various years.

will make it easier to process krill. If successful, these innovations may justify an increase in Antarctic fishing effort in coming years.

In the Black Sea and inland waters, the Soviet fishery has stagnated. The Soviet Union has the potential to become a major producer of cultured fish, yet inland fisheries and cultured production have actually declined in recent years.

North America

The North American catch totaled 6.6 million t in 1986, a 5 percent increase over the 6.3 million reported in 1985. Data on the U.S. and Canadian fish catch are illustrated in Figure 10. Geographically, Mexico is located on the North American continent, but for sociological reasons, the Mexican catch has been included in the Latin American totals.

United States

The U.S. fish catch hit 4.9 million t in 1986, a 2 percent increase from the 4.8 million t reported in 1985[8]. While the overall catch increase was not large, specific fisheries exhibited some sharp fluctuations. Catches of Alaska pollock, shrimp, and crab increased, but catches of other important species such as menhaden, Pacific salmon, and cod declined. A variety of resource and marketing problems caused most of the declines. The salmon catch declined after records set in previous years, but 1986 was still above normal.

Canada

Canada's fisheries catch is slowly recovering, following a period of decline caused by heavy fishing off Canada's Atlantic coast. During 1986, Canadian fishermen caught 1.4 million t of fish and shellfish, an increase of 16 percent over the 1.2 million t caught in 1980. Canada's most important fishing grounds lie off the Atlantic coast, contributing 1.2 million t, or two-thirds of the total catch. Top groundfish and pelagic species landed in 1986, by quantity, were Atlantic cod (457,000 t), Atlantic herring (177,000 t), various flatfishes (85,000 t), redfish (75,000 t), and capelin (65,000 t). The top mollusk and crustacean species, by quantity, were scallops (56,000 t), snow crab (42,000 t), and lobster (35,000 t).

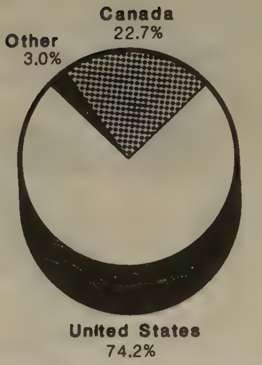

Figure 10.—North American fisheries catch, 1986; total for 1986 was 6.6 million t.

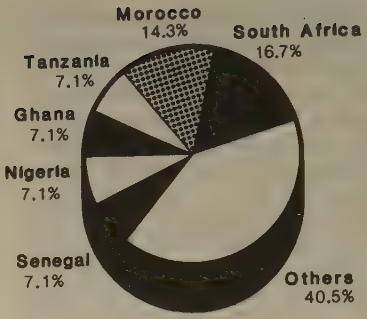

Figure 11.—African fisheries catch, 1986; total for 1986 was 4.2 million t.

The International Court of Justice decision to award the disputed rich fishing grounds off Georges Bank to Canada (prior to this decision, both the United States and Canada were allowed to fish in the contested area off of Georges Bank), strict enforcement measures on fishing by domestic and foreign fleets in Canadian waters, and rigid management plans imposed on the stocks, have helped to increase Canadian catches in recent years, although many stocks remain depressed. Despite lower catches, the value of Canadian fishery landings has helped produce record incomes for Canadian fishermen, thanks to the strong demand for fishery products in the United States and on world markets. In 1986, the Canadian catch was valued at almost C$1 billion.

Africa

The African fisheries catch has fluctuated between 4.1 and 4.4 million t since 1980. The 1986 catch was 4.2 million t, up slightly from the figure reported in 1985. African countries report a very small part of the world fisheries catch. In 1986, the African catch comprised only 5 percent of the world total, down 6 percent from 1980. The decline is a result of expanded fisheries in other areas, while African fisheries have experienced little growth. African catch data, however, do not include the extensive distant-water catch of the Soviet Union and other countries off the continent. The distant-water catch in 1985 totaled about 2.8 million t, which comprises about one-third of the total catch taken from African waters.

Seven countries (South Africa, Morocco, Tanzania, Ghana, Nigeria, Senegal, and Uganda) comprised nearly 60 percent of the 1986 African catch (Fig. 11). South Africa and Morocco are the two most important countries, and they accounted for about 25 percent of the African total, with 1986 catches of 0.7 million t and 0.6 million t, respectively. In 1985, Cape hake accounted for about 25 percent and anchovy about 40 percent of the South African catch; presumably, the composition of the 1986 catch is similar. In 1986, the sardine fishery supplied over 40 percent of the Moroccan catch, with mackerel accounting for nearly 20 percent. The remaining five countries each had 1986 catches in excess of 0.2 million tons each. South Africa's catch was stable, increasing by only 1 percent in 1986. Morocco's 1986 catch increased 25 percent, primarily because because its leading fishery for sardines increased an impressive 50 percent, according to statistics supplied by Morocco's Institute Scientifique des Peches Maritimes.

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[8] The preliminary U.S. catch data reported by FAO differs from "Fisheries of the United States, 1986," primarily because FAO calculates the live weight of mollusks while the United States calculated only the weight of the edible meats.

Middle East

Middle Eastern fishermen reported a catch of only about 1 million t in 1986. The small Middle Eastern catch is probably a combination of limited resources and lack of interest in developing the available resources. While small by world standards, the 1986 Middle East catch represented an increase of 25 percent over the 0.8 million t taken in 1980. Most of that increase occurred by 1982 and since then the catch has been stable at about the 1 million t level. The leading country in the region is Turkey, with a 1986 catch of 0.6 million tons. The Turkish catch has increased by nearly 35 percent from the 0.4 million t reported in 1980. European anchovy and horse mackerel made up about 70 percent of the catch in 1985.

Oceania

Fishermen in Oceania reported a catch of about 0.6 million t in 1986. The two major fishing countries are New Zealand (0.3 million t) and Australia (0.2 million t). New Zealand fishermen have reported steady growth since the early 1970's and achieved a new record catch in 1986. Much of the recent increase has come from expanding fishing effort to offshore fisheries and by careful management of the heavily fished coastal resources. Australian fishermen reported catch declines in 1985 and 1986. New management measures enacted to protect heavily fished stocks account for much of the decline.

Major Countries

World fisheries are dominated by 16 major countries which accounted for 75 percent of the catch in 1986 (Table 7). The two leading countries were Japan (11.9 million t) and the Soviet Union (11.1 million t). Other leading countries included China (7.3 million t), Chile (5.6 million t), Peru (5.3 million t), and the United States (4.9 million t). All have reported catch increases since 1980. The Soviet and Japanese increases are interesting as both countries heavily fish their own coastal waters and have also had to adjust to restrictions on their distant-water grounds by many coastal countries. The large increases reported by Peru and Chile were primarily due to a resurgence of the anchovy stock. While most of the principal fishing countries have reported catch increases in 1986, a few countries have reported declines: Norway (−10 percent), Iceland (−6 percent), and Thailand (−5 percent). The Norwegian trend in particular continues a trend begun in 1978. Major fishery developments in Japan, China, Chile, and Peru follow (U.S.S.R. developments were reported in a previous section).

Japan is the world's leading fishing nation, harvesting over 11.9 million t in 1986 (12.6 million t according to preliminary Japanese Government statistics), 13 percent of the world's catch. The 1986 catch is nearly a 4 percent increase over the 1985 catch of 11.5 million t and is second only to Japan's all-time record catch of 12 million t in 1984. Japan's catch has remained relatively stable since 1983, averaging about 11.7 million t annually.

Increasing enforcement of foreign 200-mile exclusive economic zones has kept Japan's distant-water catch fluctuating around 2.1 million t since 1979, with little possibility for growth. This factor has forced Japan to reevaluate its fishing strategy and to begin to fully develop its offshore and coastal resources, take a renewed look at aquaculture, and seek new fishing agreements with other countries. Although coastal production remained stable in 1986, marine culture and offshore fisheries grew by 9 percent and 5 percent, respectively. Sardines accounted for the largest increase in Japan's 1986 catch. Japanese fishermen caught about 4.5 million t, 9 percent more than in 1985. Sardine harvests in the waters off eastern Hokkaido and northern Honshu (both in the Sea of Japan and the Pacific) increased significantly in 1986. Other important species were Alaska pollock (1.4 million t), and Spanish mackerel (955,000 t); skipjack tuna registered the largest percentage increase in 1986, up 34 percent to 420,000 t.

China is the third largest fishing

Iceland's Fish Catch Steady, Value Climbs

Iceland's fisheries catch reached 1.7 million t in 1986, slightly less than Iceland's record 1985 catch. The value of the catch increased from $312 to $458 million. The cod catch again proved plentiful (366,000 t vs. 323,000 t) and the shrimp harvest rose by 44 percent from 25,000 t to 36,000 t, while the capelin catch (used mostly for reduction) declined from 993,000 t to 895,000 t. Large catches, high world prices, low oil prices, and a relatively low rate of inflation made 1986 a prosperous year for the Icelandic fishing industry. The debate over the pros and cons of fresh fish sales to Western Europe continued as representatives of the freezing industry expressed concerns over declining supplies of raw materials to meet demand for processed fishery products, mostly in the United States.

The U.S. market declined to 25 percent of the value of total Icelandic fish exports in 1986, while the continued growth in Icelandic sales to the United Kingdom makes it Iceland's most important market. The U.S. Embassy in Reykjavik has prepared an 11-page report reviewing Iceland's fisheries in 1986. The report includes sections on Iceland's fish, catch, the debate over fresh versus frozen fish sales, the growth of the United Kingdom market, foreign fishing in Icelandic waters, and the outlook for 1987. The report also includes statistical tables on Iceland's fish catch and how it is utilized, exports of fishery products by destination, exports by product form, exports to the United States, and Iceland's fishing fleet and number of fishermen. U.S. companies can obtain a copy of "Iceland's Fisheries, 1986" for $9.95 and a $3.00 handling fee (total of $12.95, personal checks or money orders only) by ordering report PB88-114566/GBA from NTIS, Springfield, Virginia 22161. (The handling fee is per order, regardless of how many reports are ordered.)

nation in the world, behind the Soviet Union, with a catch of over 7.3 million tons in 1986. The Chinese reported steady growth in all sectors of its fishing industry in 1986. The marine fisheries catch increased by 12 percent, to 3.9 million t. Principal marine species caught were croaker, hairtail, filefishes, mackerel, and shrimp. Equally spectacular growth was recorded by the freshwater fishery sector (+12 percent to 530,000 tons), marine aquaculture (+12 percent to 797,000 t), and freshwater aquaculture (+24 percent to 2.9 million t). Although China is a relative newcomer to high-seas fishing, its distant-water fleet has grown from about a dozen vessels fishing off West Africa in 1985 to over 30 fishing in the economic zones of seven countries by the end of 1986.

Despite this development, the prognosis is not overly optimistic for continued growth of China's marine fisheries sector. China's 1987 marine fisheries catch was expected to remain about the same as the 1986 catch. Chinese Government officials have predicted that fisheries production would reach 9 million t by 1990, with most of the increase coming from aquaculture. The breakthrough is expected to come in marine farming, with an estimated growth rate of over 11 percent per year. Major cultured marine species will include giant sea perch, shrimp, abalone, clams, mussels, scallops, sea cucumbers, and kelp. The main species used in freshwater culture are carp and tilapia.

Chile is the fourth most important fishing country with a 1986 catch of 5.6 million t. The fishing industry has been the fastest growing sector of the Chilean economy over the past 10 years. Officials were relieved that the 1986-87 El Niño did not adversely affect the 1986 catch, but were concerned about declining catches in 1987. Catches of the two most important species over the past few years (sardines and jack mackerel) declined in 1986, but were more than offset by increased anchovy catches. Most of the catch is reduced to fish meal, and Chile has become the world's leading fish meal exporter. Most companies are reporting good results, even though fish meal prices were substantially below 1980 price levels in constant dollars. While the large fish meal companies reported good results, Chilean fishermen reported declining catches in several traditionally important fisheries (shrimp, sea snails, sea urchins, langostinos, and several other valuable shellfish) in 1986. Other fishermen reported several promising developments in 1986, including expanded harvests of cultured salmon, small-scale surimi production, increased krill landings, and expanded landings of high quality fresh fish for the export market.

Peru was the fifth leading fishing country in 1986 with a catch of 5.3 million t. Peruvian fishermen reported a massive 25 percent increase over their 1985 catch. The increase was primarily due to the resurgence of anchovy stocks. Fishermen in northern Peru were affected by the 1986-87 El Niño beginning in late 1986. Fishermen along the central and southern coast did not begin to report catch declines, however, until mid-1987. (It is not known to what extent the declining 1987 catches in Peru and Chile were due to El Niño or other factors such as overfishing.) While the El Niño was affecting 1987 catches, most of Peru's reduction plants and canneries reported substantially improved results for 1986. The Government gave special priority to efforts aimed at increasing the catch of edible fish to increase supplies to the domestic market. An agreement was signed with Cuba to permit Cuban distant-water trawlers to operate in Peruvian waters and land their catch in Peru. The Government also provided funding so that the state food fish company, the Empresa Publica de Servicios Pesqueros (EPSEP), could acquire its own fishing fleet. Even though catches increased sharply, several long-standing problems plagued the industry in 1986, including labor strife, unused canning capacity, the inability to reach an agreement with the Soviets on joint ventures, high interest rates, low fish meal prices, and a sharp decline in scallop catches.

Aquaculture

While some have predicted that aquaculture, sometimes referred to as the "blue revolution," would rapidly replace wild capture fisheries (which many expected to decline), this has not proven to be the case. Capture fisheries have not declined, nor has aquaculture begun to account for more than a small share

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Atlantic Canada's Aquaculture Industry

Atlantic Canada's 33 commercially viable fish farms produced 1,800 t of mussels, 500 t of salmon, and 110 t of trout in 1986. The leading province in Atlantic Canada's aquaculture industry is Nova Scotia (11 farms), followed by New Brunswick (9 farms), Prince Edward Island (6-8 farms), and Newfoundland (5 farms). In 1986, these aquaculture facilities generated about C$9 million and it is projected that this amount could be increased 30 times in 10 years.

Many Canadian fish farmers are short on working capital and technical knowledge. Provincial governments have limited themselves to providing technical aid, but not funding. Future expansion of aquaculture facilities is expected to be opposed by homeowners living near potential aquaculture sites. The region has limited access to processing facilities and the severity of Canadian winters are factors that need to be examined before Atlantic Canada's aquaculture industry can meet its full potential. The U.S. Consulate General in Halifax has prepared a 9-page report reviewing Atlantic Canada's aquaculture industry. The report includes sections on the scope of the industry, aquaculture legislation, funding programs, public opposition, technical problems, and comments. The report also includes list of Federal and provincial legislation in the field of aquaculture. U.S. companies can obtain a copy of "Atlantic Canada's Aquaculture Industry, 1986" for $9.95 and a $3.00 handling fee (total of $12.95, personal checks or money orders only) by ordering report PB88-114574/GBA from NTIS, Springfield, VA 22161. (The handling fee is per order.)

of the world's fisheries production. The combined total of cultured production and freshwater fisheries was only 8.4 million t in 1985, about 10 percent of the world total[9]. For the foreseeable future, fishermen will be able to catch most species in larger quantities and more cheaply than fish farmers will be able to culture them. Fish farmers have, however, reported some successes. The greatest commercial successes have come from efforts to culture high value species for luxury food markets. Efforts to culture salmon and shrimp have been particularly noteworthy. The Branch of Foreign Fisheries Analysis estimates that fish farmers harvested about 70,000 t of salmon and 310,000 t of shrimp in 1986. While small in quantitative terms, these are particularly valuable species and many observers believe that production will increase far beyond current levels. Other fish farmers have reported success with catfish, trout, mullet, oysters, and mussels. Experimental work is currently underway on a wide range of other species. In some cases, however, fish farmers will not increase the total world supply of food. Many fish farmers, for example, use low-value fish to feed the species which they are culturing. The operation is profitable, but may not result in a net increase of edible commodities. Several developing countries have pursued projects to culture tilapia, carp, mullet, and various other species. Some of these projects have resulted in increases of edible commodities. Increases in carp and tilapia catches and Asian catches of a wide variety of freshwater species suggest that aquaculture is gradually increasing the production of edible fish in developing countries, although statistical data separating aquaculture and freshwater fisheries is not readily available.

The Latin American Shrimp Culture Industry

Latin America is a leading world producer of cultured shrimp. Shrimp farmers in the region harvested over 50,000 t of shrimp in 1985, a 40 percent increase over the 37,000 t of shrimp cultured in 1985. Ecuador dominates the region's shrimp culture industry—nearly 85 percent of the Latin American harvest was produced in that country. The industry continues to expand in Ecuador and is rapidly growing in several other countries as well. Prospects for the development of important shrimp culture industries are especially good in Brazil and Colombia.

Ecuador reported major increases in pond harvests during 1987. Several other countries also reported substantial, if less spectacular, 1987 harvests. Based on these increases and continuing expansion of the industry, the NMFS Branch of Foreign Fisheries Analysis conservatively estimates that the cultured shrimp harvest in Latin America could reach nearly 115,000 t by 1990. That projection is based primarily on one country (Ecuador) and one species (*Penaeus vannamei*). As more countries enter the industry and technical advances enable farmers to increase yields and perhaps use different species of shrimp, it is likely that production will continue to increase during the 1990's. Many observers are unsure, however, about the impact of rising world production on the international shrimp market. If substantially lower prices result from the increased production, profit margins could be significantly affected. If so, many farmers may have to adjust their production and expansion plans.

The NMFS Branch of Foreign Fisheries Analysis has prepared an 80-page report reviewing the current status of the shrimp culture industry in Latin America. The report covers: harvest levels, the regional importance, traditional fisheries, quality/size control, species, government support, postlarval seedstock, variables (economic, technical, environmental, and political), investments, and a separate section on each country. The report includes extensive statistical appendices on harvests and exports and is a slightly updated version of the Latin American section in the U.S. Department of Commerce's "Aquaculture and Capture Fisheries: Impact in U.S. Seafood Markets," published earlier in 1988. U.S. companies can obtain a copy of "Latin American Shrimp Culture Industry, 1986-90" for $14.95 and a $3.00 handling fee (total $17.95, personal checks or money orders only) by ordering report PB88-210745/GBA from NTIS, Springfield, VA 22161.

Potential

The world potential fish catch of edible species has been debated for some years. One widely accepted—although not undisputed—estimate in the world fisheries community, is that the world catch will continue to increase until about the year 2000 when it could total 100-120 million t of conventional species, a figure that many experts believe is the approximate maximum world yield. These estimates may have to be revised. If current trends continue, the 100 million t figure could be reached as early as 1990. However, several Latin American countries have reported declining catches in 1987, principally due to El Niño. Year-end results for the entire world may be about the same as or a small decline from 1986 figures.

Projections of future fish catches, however, are tenuous at best. A wide variety of factors will affect actual increases: Fuel prices, interest rates, national management and development measures, fish prices, technological developments, interest rates, and other developments. Many biologists currently believe that conventional stocks will not support catches significantly beyond the 120 million t level.

Further increases could, however, come from species not currently being utilized. If profitable ways of utilizing Antarctic krill, for example, could be developed, the world catch could expand significantly beyond the 100-120 million t level. Some experts have projected that an intensive krill fishery could double or triple the world catch, but more recent assessments have been more conservative. The 1985 krill catch was less than 0.2 million tons, mostly taken by the Soviets who have been reducing fishing effort in recent years.

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[9] Precise data on cultured harvests are not readily available, but the Branch believes that a rough estimate of aquaculture trends can be obtained by following catch trends in inland areas reported by FAO.

Even within existing catch levels, the production of edible products could be substantially increased. Production of edible products from fisheries could be expanded by better utilizing existing catches. About 30 percent of the catch is currently used for reduction fisheries producing fish meal and oil. Animal feed, of course, is not lost to human consumption as most of the animals will be slaughtered for food. The amount of protein available, however, would be increased if the fish were consumed directly instead of being used for fish meal production. Perhaps as much as 10 percent of the world catch is lost as a result of poor handling and processing procedures. Many fishermen discard large quantities of unwanted fish at sea. Suggestions concerning utilization of fish currently reduced to fish meal, landing species currently discarded, improved handling, and other measures to increase food production are often presented in unrealistic terms. They must be tempered by economic reality. Processors must be able to produce a product that will appeal to consumers at affordable prices. (Source: IFR-87/63.)

Argentine Fisheries See Good Growth

Argentine fishing companies reported an excellent year in 1986. Higher international prices and the emergence of Brazil as a major buyer in the third quarter of 1986 were crucial factors in Argentina's improved 1986 export performance. Argentine fishery exports totaled $219 million in 1986, an 110 percent increase over the $104 million exported in 1985. Several long-term difficulties still plagued the Argentine fishery industry in 1986: An outdated fleet, limited port facilities, outmoded processing plants, and inefficient infrastructure, all of which prevented an even better performance. The Argentine Government has instituted some assistance programs for the fishing industry. Several companies were able to put vessels back into service during 1986 by taking advantage of a new credit line offered by the Argentine Development Bank which was designed to promote the renovation of the fleet. The Government also signed fishery agreements with Bulgaria and the Soviet Union which, it hopes, will result in export sales to the Soviet Union and Eastern Europe.

The U.S. Embassy in Buenos Aires has prepared a 24-page report reviewing the current status of Argentina's fishing industry. The report includes sections on landings, industry performance, economic conditions, foreign fishing, port facilites, fishing fleet, markets, and production. The report also includes extensive tables, including data on catch, exports, biomass, maximum sustainable yields, and fleet. There is also a list of Argentine fishery associations. U.S. companies can obtain a copy of "The Argentine Fishing Industry, 1986" for $11.95 and a $3.00 handling fee (total $14.95, personal checks or money orders only) by ordering report PB88-114475/GBA from NTIS, Springfield, VA 22161.

Open-Sea Salmon Farm Is Started off Norway

What Norwegian authorities describe as the world's first fish farm for salmon in the open sea, began operation in late April to the west of the island of Værøy, one of the Lofoten Islands off north Norway. The small fry have to be set out in June, and the first artificially cultivated deep sea salmon should be on the market next year, reports Norinform.

The development of the farm, budgeted at US$670,000, was planned in cooperation with industry in north Norway, and based on the technology used in the offshore sector. The depth of water at the farm will be more than 100 m, and waves up to 13 m in height have been measured at the location. The plant has therefore been dimensioned to tolerate wave heights up to 22 m. The facilities will comprise 20 enclosures firmly anchored to the seabed by heavy weights, and totalling 23,000 m^3, vs. the normal coastal farm size of 8,000 m^3. A ship anchored at the plant will steer operations.

The initiators took advantage of the fact that the location of the farm is outside the 4-mile concession limit. A spokesman for the Ministry of Fisheries has stated that the ministry may consider changes in legislation so that farms outside normal 4-mile limits also must comply with regulations. Free access for the establishment of fish farms in open sea conflicts with the intention of the law, which is to regulate such establishments out of consideration to public interests, says Gunnar H. Gundersen of the Ministry of Fisheries.

New NMFS Scientific Reports Published

The publications listed below may be obtained from either the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 or from the National Technical Information Service, Springfield, VA 22151. Writing to the agency prior to ordering is advisable to determine availability, order numbers, and price.

NOAA Technical Report NMFS 54. Gooch, Janet A., Malcolm B. Hale, Thomas Brown, Jr., James C. Bonnet, Cheryl G. Brand, and Lloyd W. Regier. **"Proximate and Fatty Acid Composition of 40 Southeastern U.S. Finfish Species."** June 1987, iii + 23 p., 43 tables.

ABSTRACT

This report describes the proximate composition (protein, moisture, fat, and ash) and major fatty acid profiles for raw and cooked samples of 40 southeastern finfish species. All samples (fillets) were cooked by a standard procedure in laminated plastic bags to an internal temperature of 70°C (158°F). Both summarized compositional data, with means and ranges for each species, and individual sample data including harvest dates and average lengths and weights are presented. When compared with raw samples, cooked samples exhibited an increase in protein content with an accompanying decrease in moisture content. Fat content either remained approximately the same or increased due to moisture loss during cooking. Our results are discussed in reference to compositional data previously published by others on some of the same species. Although additional data are needed to adequately describe the seasonal and geographic variations in the chemical compositions of many of these fish species, the results presented here should be useful to nutritionists, seafood marketers, and consumers.

NOAA Technical Report NMFS 55. Krzynowek, Judith, and Jenny Murphy. **"Proximate Composition, Energy, Fatty Acid, Sodium, and Cholesterol Content of Finfish, Shellfish, and Their Products."** July 1987, iii + 53 p., 2 tables.

ABSTRACT

This document contains data concerning the proximate composition and energy, fatty acid, sodium, and cholesterol content of finfish, shellfish, and their products, as listed

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The Management of Migratory Fishes

"Multi-Jurisdictional Management of Marine Fisheries." edited by Richard H. Stroud, constitutes the "Proceedings of the Eleventh Annual Marine Recreational Fisheries Symposium" held in Tampa, Fla., in May 1986, and is published by the National Coalition for Marine Conservation, Inc., Savannah, Ga. Frank E. Carlton set the tone for the symposium with his introductory address "Fish Know No Boundaries," which was followed by then-NOAA Administrator Anthony J. Calio who assessed the Federal role in marine fisheries. Carl E. Nettleton then addressed the development of a fisheries resource management plan that would achieve optimum population levels. As with the earlier symposia, this one divided the presentations into several Panels: 1) Putting the challenge of fisheries management into perspective, 2) inter-jurisdictional problems, 3) case studies, 4) new directions for management, 5) to preempt or not, 6) NMFS, Councils, and the Act (MFCMA), ending with summaries of each panel's by the panel chairmen.

In large part, the presentations address the problems and opportunities in managing marine and anadromous fishes under the MFCMA by the various Councils; another important aspect covered was management by the creation of habitat for certain species. In addition, some very controversial issues were aired, including Federal preemption of state authority, Federal saltwater fishing licenses, the Native American role in fisheries management, and various interjurisdictional fisheries problems. In addition, floor discussions and panel debates are published which help air various sides of the issues. Case studies presented included discussions of state-Federal management of red snapper and gag; multi-state-Federal management of king mackerel, and international management of highly migratory tuna and billfishes. Unindexed, the hardbound volume is available from the International Game Fish Association, 3000 East Las Olas Blvd., Ft. Lauderdale, FL 33316-1616 for $15.00.

Game Fish Trophies, Articles Published

"World Record Game Fishes 1988" has been published by the International Game Fish Association, 3000 East Las Olas Blvd., Ft. Lauderdale, FL 33316-1616, under the direction of Elwood K. Harry. This year the "articles" section is devoted to presentations by four noted outdoor writers on some of the world's finest angling areas: Alaskan angling by Chris Batin, Hawaiian offshore fishing by Jim Rizzuto, Australia's Great Barrier Reef trophies by Peter Goadby, and America's blue-ribbon trout streams by A. J. McClane.

Also rewritten this year and considerably updated is the game fish species section, about 6 pages of data on popular fishes and which includes many new and improved illustrations, a number by NMFS biologist-artist Susan Smith.

in 228 articles published between the years 1976 and 1984. Also included is a systematic index of the species as referenced in this document listed alphabetically by scientific names.

NOAA Technical Report NMFS 56. Hirth, Harold F., and Larry H. Ogren. **"Some Aspects of the Ecology of the Leatherback Turtle *Dermochelys coriacea* at Laguna Jalova, Costa Rica."** July 1987, iii + 14 p., 13 figs., 12 tables.

ABSTRACT

The ecology and reproductive biology of the leatherback turtle (*Dermochelys coriacea*) was studied on a high-energy nesting beach near Laguna Jalova, Costa Rica, between 28 March and 8 June 1985. The peak of nesting was between 15 April and 21 May. Leatherbacks here measured an average 146.6 cm straightline standard carapace length and laid an average 81.57 eggs. The eggs averaged 52.12 mm diameter and 85.01 g weight. Significant positive relationships were found between the carapace lengths of nesters and their clutch sizes and average diameter and weight of eggs. The total clutch weighed between 4.02 and 13.39 kg, and yolkless eggs accounted for an average 12.4 percent of this weight. The majority of nesters dug shallow (<24 cm) body pits and spent an average 81 minutes at the nest site. A significant number of clutches were laid below the berm crest. In a hatchery 42.2 percent of the eggs hatched, while in natural nests 70.2 percent hatched. The average hatchling carapace length was 59.8 mm and weight was 44.6 g. The longevity of leatherback tracks and nests on the beach was affected by weather. One nester was recaptured about 1 year later off the coast of Mississippi. Egg poaching was intense on some sections of the Costa Rican coast. Four aerial surveys in four different months provided the basis for comparing density of nesting on seven sectors of the Caribbean coast of Costa Rica. The beach at Jalova is heavily used by green turtles (*Chelonia mydas*) after the leatherback nesting season. The role of the Parque Nacional Tortuguero in conserving the leatherbak and green turtle is discussed.

NOAA Technical Report NMFS 57. Brodeur, Richard D., Harriet V. Lorz, William G. Pearcy. **"Food Habits and Dietary Variability of Pelagic Nekton off Oregon and Washington, 1979-1984."** July 1987, iii + 32 p., 1 fig., 32 tables.

ABSTRACT

The food habits of 20 species of pelagic nekton were investigated from collections made with small-mesh purse seines from 1979-84 off Washington and Oregon. Four species (spiny dogfish, *Squalus acanthias*; soupfin shark, *Galeorhinus zyopterus*; blue shark, *Prionace glauca*; and cutthroat trout, *Salmo clarki*) were mainly piscivorous. Six species (coho salmon, *Oncorhynchus kisutch*; chinook salmon, *O. tshawytscha*; black rockfish, *Sebastes melanops*; yellowtail rockfish, *S. flavidus*; sablefish, *Anoplopoma fimbria*; and jack mackerel, *Trachurus symmetricus*; consumed both nektonic and planktonic organisms. The remaining species (market squid, *Loligo opalescens*; American shad, *Alosa sapidissima*; Pacific herring, *Clupea harengus pallasi*; northern anchovy, *Engraulis mordax*; pink salmon, *O. gorbuscha*; surf smelt, *Hypomesus pretiosus*; Pacific hake, *Merluccius productus*; Pacific saury, *Cololabis saira*; Pacific mackerel, *Scomber japonicus*; and medusafish, *Icichthys lockingtoni*) were primarily planktonic feeders. There were substantial interannual, seasonal, and geographic variations in the diets of several species due primarily to changes in prey availability. Juvenile salmonids were not commonly consumed by this assemblage of fishes.

Revised and updated, too, are the sections on international angling rules and world record requirements—particularly with the new additions to the world record eligible list like the queenfish, Japanese seabass, kahawai, bluefin trevally, and mutton snapper. For avid anglers, the "meat" of the publication is the listings of world angling trophies (freshwater and saltwater), plus fly-rod and all-tackle trophies and membership in the Thousand Pound Club and the 5, 10, and 20-to-1 clubs. Also provided are lists of state game fish record keeping agencies and organizations, worldwide recordkeeping organizations, and tag-and-release programs. The 320-page paperbound volume is available from the publisher for $9.75 (U.S.) and $11.95 (foreign).

Pacific Salmon and Their Management

Publication of **"Salmon Production, Management, and Allocation,"** edited by William J. McNeil, has been announced by the Oregon State University Press, 101 Waldo Hall, Corvallis, OR 97331-6407. Subtitled "Biological, Economic, and Policy Issues," it is a compilation of 20 papers presented at the World Salmonid Conference which was held in October 1986 in Portland, Oreg., by the Salmonid Foundation. The authors, ranging from scientists and aquaculturists to economists, fishery managers, and lawyers, have presented a wide variety of authoritative papers relating to the integration of aquaculture into the overall production of Pacific salmon, and the topics range from salmon biology and ecology to pertinent social and economic issues.

Lawyer Alfred A. Hampson discusses the laws and property rights relating to salmon ranching by public and private entities, and he suggests several legislative needs. A thorough review of Japanese salmonid programs, salmon supplies, and public policy is given by Yoshio Nasaka, while Frank Gjerset reviews the status and outlook for Norwegian Atlantic salmon farming, comparing characteristics of that industry with those of the U.S. catfish farming industry. Other articles include changes in the catch pattern of North American salmonids by Japan's high seas fleet by Colin Harris, while William Pearcy discusses factors affecting survival of coho salmon off Oregon and Washington, and Ernest Salo looks at the chum salmon as an indicator of ocean carrying capacity. And, Donald Rogers reviews the timing and size composition of Bristol Bay smolt migrations and the effects on distribution and survival at sea.

Additional papers discuss the problems involved in managing mixed-stock salmon fisheries; the culture, allocation, and economic value of Pacific salmon in the Great Lakes; conservation and allocation decisions in fishery management, the impacts on coastal communities of recreational-commercial fishery allocation of salmon; salmon markets, economics of recreational salmon fishing, potential hazards for spreading of infectious disease by transplanted fish, and directed and inadvertent genetic selection in salmonid culture.

Salmon harvests, after dropping to less than half their historic levels, began increasing nearly two decades ago, and are again approaching their historic levels. While naturally produced salmon still contribute most to the world's salmon harvest, aquaculture production is growing rapidly. This book examincs many important issues, some very controversial, and should be of interest to those involved in salmon research, culture, marketing, and management. Indexed, the 194-page hardbound volume is available from the publisher for $31.95 postpaid.

The Marine Fisheries of Indonesia and Thailand

The International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines, has produced excellent new reviews on the fisheries of Thailand and Indonesia. **"Indonesia Marine Capture Fisheries"** by C. Bailey, A. Dwiponggo, and F. Marahudin, ICLARM Contribution 338, is part of the ICLARM Studies and Reviews Series 10. The authors have winnowed existing literature to provide a fine descriptive overview of that nation's fisheries and, in the process, pointed out areas in need of greater study and research. Following reviews of the nation's marine fisheries and fishery resources, the authors address fisheries management and development policies and programs, economics, fish marketing and distribution, socioeconomic factors of small-scale fisheries, and needs for further research. Included in the 196-page paperbound volume is an extensive list of references. The volume is available either from ICLARM at US$9.50 (surface mail) or US$18.00 (airmail) or, in the United States, from International Specialized Book Services, P.O. Box 1632, Beaverton, OR 97075 at $18.00.

ICLARM Technical Reports 17 is **"Growth, Mortality and Recruitment of Commercially Important Fishes and Penaeid Shrimps in Indonesian Waters"** by A. Dwiponggo, T. Hariati, S. Banon, M. L. Palomares, and D. Pauly. Data is presented in 61 plates and tables covering fishes ranging in size from 10 cm (*Secutor ruconius*) to 80 cm (*Katsuwonus pelamis*) and for areas from Jakarta Bay to the Arafura Sea. Altogether, 52 stocks of fish are covered, including 36 species, 21 genera, and 15 families of bony fishes as well as 9 annual cohorts from the Arafura Sea stock of the shrimp *Penaeus merguiensis*. Presented are estimates of von Bertalanffy growth parameters which were derived through application of the ELEFAN I program to length-frequency data from the various fishes. Derived quantities such as total, natural, and fishing mortality estimates, as well as selection and recruitment patterns were then obtained by application of the ELEFAN II program to the same length-frequency data. Some generalizations on the status of the stocks are presented, particularly for the demersal fishes off the north coast of Java and on *P. merguiensis* in the Arafura Sea. Paperbound, the 91 page volume is priced at US$4.50 (surface mail) and US$8.50 (airmail and the U.S. price from ISBS).

ICLARM Studies and Reviews 14 is **"The Economics and Management of Thai Marine Fisheries"** by Theodore Panayotou and Songpol Jetanavanich. Like number 10, this is a fine review of the relevant literature and presentation of data on Thai fisheries—one of the world's ten largest, having a fleet of more than 20,000 modern vessels and a harvest of around 2 million metric tons. Thailand fishermen supply 20 kg/capita of fish for a population of 50 million and earn the nation about $500,000,000 in foreign exchange annually. The authors document the profitability of the trawl fishery, small-scale fishermen's economic problems, overfishing in the Gulf of Thailand, and the problems and potential in the nation's management and enforcement capabilities. It also suggests a number of solutions to Thai fisheries problems. Price of the 82-page paperbound volume is US$5.00 (surface mail) and US$9.00 (airmail—and the ISBS price). ICLARM recommends orders to them be for airmail delivery owing to surface mail delays of several months and potential losses in transit.

ICLARM has also published ICLARM Bibliographies 7, "A Bibliography of Trochus (*Trochus niloticus* L.) (Gastropoda: Trochidae), by Warwick J. Nash, updating the annotated bibliography of Gail and Devambez of 1958. It includes over 130 citations, many hard to locate in conventional databases, along with subject and geographic indexes (price not listed).

What Is Ecology?

When Danish marine ecologist and professor Tom Fenchel received the first annual "Excellence in Ecology" award from the Ecology Institute, Oldendorf/Luhe, FRG, he found a string attached: He was expected to serve science and society by authoring a book along the aims of the Institute. Thus, the first book in the new series "Excellence in Ecology" is Fenchel's **"Ecology—Potentials and Limitations,"** edited by O. Kinne, Institute Director. Fenchel's book is aimed primarily at other ecologists, hoping to engage them in a debate on the definition of ecology, as well as to present central problems and results of ecology to biologists at large and to other scientists.

The author complains that ecology, per se, seems to be a "diffuse" or an "immature" science that many people would define differently, often in light of their own specialization. He notes that ecology differs from most other natural sciences in seemingly lacking a central core of ideas, concepts, methods, and goals upon which everyone can agree. Fenchel then strives to present what he sees as the "core" of that discipline, and to provide a synthesis of the field.

In so doing, the author begins with a brief historical background of contemporary ecology and presents his view of how ecology should be defined: "As the study of the principles which govern temporal and spatial patterns for assemblages of organisms." He discusses different types of theoretical models used in ecology and attempts to delimit ecology relative to other biological disciplines, such as natural history, evolutionary biology, physiology, behavioral biology, and biogeochemistry.

Section III, entitled "Concepts, ideas, and problems in ecology," presents a more detailed look at the "gist" of ecology—scales of size and time among living things, flow of energy and materials, resource competition, interactions between species populations, structure of biotic communities, evolution of life cycles, and more. The following section (IV) then presents selected examples to illustrate several of the general ecological principles given in the previous section.

Section V, "Ecology and society," is concerned with applied ecology, and here Fenchel warns his peers that, while applied research is necessary and desirable, some aspects of ecology may be especially vulnerable to intellectual corruption. This is an especially thoughtful and interesting book, made all the more so because of the author's marine science background and the examples woven through it. The 186-page hardbound volume is available from the publisher, Ecology Institute, D-2124 Oldendorf/Luhe, Federal Republic of Germany; price is DM7, or about US$40 (depending on the exchange rate).

A Trolling Handbook for South Pacific Fishermen

"Trolling Techniques for the Pacific Islands," by G. L. Preston, L. B. Chapman, P. D. Mead, and P. Taumaia and illustrated by S. E. Belew is Handbook No. 28 of the South Pacific Commission, Noumea, New Caledonia. The handbook was developed as a training aid for the Pacific Island region to document some of the specialized and often unwritten knowledge and practical experience gleaned by SPC staff over the years, and the latter may be its greatest strength. The volume is thoroughly and well illustrated and clearly documents many of the techniques learned or proven in that region over the years.

Following a basic introduction to Pacific trolling, the authors illustrate, chapter by chapter, all aspects of that fishery for the individual small-scale fisherman: Vessel considerations and preparation (fish containers, trolling booms, handreels, gaffs, etc.); preparation of trolling lines and gear; types of baits and lures and their rigging; trolling conditions and techniques; fishing action—working the lines, the strike, handling fish on fixed lines and handreels, and boating and care of the catch; care of the boat and fishing gear and recordkeeping; coping with problems—injuries, accidents, breakdowns, signalling, and sea survival techniques. Another chapter describes the habits and characteristics of commonly caught species; appendices illustrate pole trolling in the Pacific Island tradition and give suggestions for additional sources of information. All in all, the book is an excellent guide for the region's fishermen. Paperbound, the 162-page volume is available from the SPC (price not listed).

Drying of Fish With Solar Energy

Drying fish is an ancient preservation method that is still of considerable importance, especially in tropical regions. Aspects of this, and appropriate techniques and research, are addressed in **"Solar Drying in Africa,"** subtitled Proceedings of a Workshop held in Dakar, Senegal, 21-24 July 1986, edited by Michael W. Bassey and O. G. Schmidt and published by the International Development Research Center, P.O. Box 8500, Ottawa, Canada K1G 3H9. Contributions address a range of studies including papers reviewing solar energy available in typical tropical locations and applications of solar energy in food production, and construction and performance of solar crop dryers. Studies are presented on the evaluation of various types of solar dryers—solar concentrator/dryer, flat-plate collector/dryer, and flat-plate collector/dryer-storage unit.

Another paper specifically addresses appropriate technology for solar drying of salt fish and fermented fish. Others discuss the application of natural- and forced-convection style solar dryers to various fishes and fish products, along with other agricultural commodities. Additional reports address the outlook for solar drying of fish in The Gambia, how solar drying can reduce post-harvest fish losses, and a variety of problems and developments in solar drying in African nations. The 286-page paperbound volume, IDRC-255e, is available from the IDRC (price not listed).

MACROALGAE AND ENERGY PRODUCTION

The energy crisis of the early 1970's spawned many efforts to gain new sources of energy; some went for deeper deposits of oil and gas, some turned to coal, and some, as the following volume attests, went to the sea, in this case to cultivate seaweeds for energy conversion. **"Seaweed Cultivation for Renewable Resources,"** edited by K. T. Bird and P. H. Benson, and published as volume 16 in the series "Developments in Aquaculture and Fisheries Science" by Elsevier Science Publishing Company Inc., 52 Vanderbilt Avenue, New York, NY 10017, goes well beyond simply reviewing seaweed as an energy source. Many of the advancements reported initially in various (and sometimes hard to locate) symposia, conference proceedings, technical reports, and journal articles are here condensed, synthesized, and collected into one volume.

The first four chapters deal with the giant kelp, *Macrocystis pyrifera*, the species which was the primary candidate in most marine biomass studies. Indeed, chapter 1 provides both a history of the giant kelp biomass program but reviews the early and current industrial development and utilization of kelp. Chapter 2 then describes successes and failures of the early efforts to cultivate kelp on offshore structures, while chapter 3 reviews the work on growing kelp in nearshore farm environments. Chapter 4 discusses the optimization of kelp growth in marine farms.

Chapter 5 then describes *Laminaria* culture in the far east and in North America, along with the idea of multicropping with a summer-adapted seaweed species for improved year-round productivity. C. K. Tseng then reviews the Chinese kelp cultivation industry and its implications for biomass energy systems.

Many other less well known seaweeds, of course, are adapted to warm water habitats and the biology of such important tropical and subtropical species are reviewed by Clinton Dawes in chapter 7, along with physiological considerations in relating to their cultivation. Biomass production of *Gracilaria* in outdoor cultivation systems in Florida is discussed in chapter 8, along with factors influencing *Gracilaria* yield, research on other species of macroalgae (i.e., *Sargassum* and *Ulva*), and a discussion of other uses for biomass of macroalgae (i.e., hydrocolloid production, wastewater treatment, fish feed, fodder, and fertilizer). Additional chapters discuss tissue culture of seaweeds, nitrogen fixation in marine communities and its potential role in seaweed cultivation, biological gasification of marine algae, microbial degradation of marine biomass, cost analyses of energy from marine biomass, and a commercialization strategy for nori culture in Puget Sound, Washington. Each chapter carries a literature cited section, and a separate section at the end of the book presents a list of 78 technical reports on marine biomass for energy, along with suggested sources of additional data or reports (i.e., symposia proceedings, etc.).

The key to the future of marine biomass programs, the editors note, must be crop yield improvements, perhaps through breeding and genetic analysis to produce new crop candidates. While western biomass to energy programs are now idle, they have generated much important and useful information which this volume handily reviews. Indexed the 381-page hardbound volume is available from the publisher.

Toward a Sociology of Natural Science

Publication of **"Social Science in Natural Resource Management Systems,"** edited by Marc L. Miller, Richard P. Gale, and Perry J. Brown, as part of the "Social Behavior and Natural Resources Series, has been announced by Westview Press, 5500 Central Avenue, Boulder, CO 80301. Some natural resource agencies seem to have integrated social scientists and their studies into research and management programs and policies more than others and this volume examines a variety of such situations—including marine fisheries.

Presentations are divided into several parts: Following an overview of natural resource management systems, the section "Roles of Science" presents a discussion of natural resource sociology, utilizing forests and marine fisheries as the examples, and the authors suggest a need to strengthen natural resource sociology to be better able to respond to shifting social, political, and economic situations. Other contributions in this section examine the partnership between social scientists and park and resource managers, the practice and promise of social science in the U.S. Forest Service, the integration of social science into wildlife management, and the sociology of the forestry and marine fisheries sciences in the Pacific Northwest.

A third section, "Applications of Social Science," has chapters on park planning in Canada, planning and managing visitor activity in Canadian National Parks, social carrying capacity research in a wilderness area, and an interesting discussion of emotions in environmental decision making—rational planning vs. the passionate public. A final section presents reports on social science research and recommendations on three public land issues.

Early on, the editors present their concept of a natural resource management system (NRMS), a four-part system with the following elements: 1) natural resources, 2) management bureaucracies, 3) profit-seeking industries, 4) and diverse publics (organized and unorganized), in which they establish all four components as fair objects of social science research. In addition, they portray "management bureaucracies" as "embedded within" the NRMS, rather than as a "detatched steward." They then utilize this NRMS as a basis for comparing resource management experiences in later chapters. The book is aimed primarily at social scientists who, the editors say, "must establish their own niche in natural resource management systems." But it would also be of interest to resource biologists and managers who must also deal with social as well as resource issues on a daily basis. Paperbound, the 265-page book is available from the publisher for $22.50.

Marine Ecology Text Updated

The second edition of **"An Introduction to Marine Ecology"** by R. S. K. Barnes and R. N. Hughes has been considerably revised and updated by authors and republished by Blackwell Scientific Publications, Inc., 667 Lytton Avenue, Palo Alto, CA 94301. The volume is intended for students with a knowledge of basic ecology, but who are venturing into marine ecology for the first time. Thus, each chapter treats a distinct process or subsystem of the ocean.

Following a general introductory chapter on the nature and global distribution of marine organisms and their habitats, the authors succinctly review the planktonic system of surface waters, the benthos of continental shelf and littoral sediments; salt marshes, mangrove swamps and seagrass meadows; rocky shores and kelp forests; coral reefs, pelagic and benthic systems of the deep sea; fish and other nekton, ecology of life histories, speciation and biogeography, the marine ecosystem as a functional whole, and human exploitation and interference. Indexed, the 351-page volume is available in paperbound ($29.50) and hardbound ($67.50) versions from the publisher, and it provides a good concise introduction to the field.

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ACCUMULATION OF AGE PIGMENTS (LIPOFUSCIN) IN TWO COLD-WATER FISHES

In fisheries management, age structured models are the preferred method for meeting the key objectives of estimating optimal yields and determining the effect of fishing on stock structure (Gulland 1978). However, few species of commercial marine fishes exist in which age can be determined with certainty (Boehlert 1985). The concentration of age pigments (lipofuscin) (Ettershank 1984) in fish tissues (Agius and Agbede 1984) may be a measure of fish age that could be used to validate other ageing techniques and might also improve estimates of age of long-lived species where other techniques are difficult to apply.

Lipofuscin originates in biological membranes through lipid peroxidation (Tappel 1975). Lipofuscin accumulation has been documented for a wide variety of animals, from mammals to the bread-mold *Neurospora* (Ettershank et al. 1983 and references therein). The rate of accumulation has been shown to be constant during the lifetime of laboratory-raised mice (Reichel 1968; Miquel et al. 1978), dogs (Munnell and Getty 1968), flesh-flies (Ettershank et al. 1983); man (Strehler et al. 1959); and also wild populations of mice (Dapson et al. 1980). On the other hand, the rate of lipofuscin accumulation has been shown to vary with level of activity and lifespan (Sohal and Donato 1978). It is expected that the rate in which lipofuscin accumulates with age in a natural population of fishes, or stock, with its free genetic interchange and likely common habitat, would be fairly uniform (but see Smith 1987). In addition, if measurements are made in nonmitotic and constantly metabolizing tissues such as brain or myocardium, the variation in concentration due to environmental effects is least likely.

In this paper we present the results of a preliminary study designed to assess the usefulness of extracted lipofuscin as a method of ageing fishes. Two species of cold-water fishes are included: the rainbow trout, *Salmo gairdneri*, reared in captivity, and of known age; and the Dover sole, *Microstomus pacificus*, a long-lived fish, in which age is not known with certainty. We present spectral characteristics of the extracted lipofuscin from several tissues and the change in concentration of lipofuscin with fish age.

Materials and Methods

Specimens of Dover sole were collected on December 1986 off Point Conception. Ages were estimated by J. Butler, E. Lynn, and M. Drawbridge of the Southwest Fisheries Center using otolith sections. Ages ranged from 2.7 to 44.7 years (average of three readings). Specimens of the species *Salmo gairdneri* were collected in July 1986 at Hot Creek Hatchery. Ages ranged from 3 months to 3 years.

Samples were frozen after collection and kept at −80°C until analysis. Studies by Nicol (1987) showed that this form of preservation yielded the lowest fluorescence when compared with ethanol and formalin-preserved samples. There was no indication that the level of fluorescence changed as a function of time of preservation or by interaction with the extracted lipofuscin, as in the case for formalin. To excise the brain, the top of the skull was opened and the four brain lobes were removed as a unit, without the optic nerve. To excise the heart, we separated the muscle from connective tissue, blood vessels, and fat deposits.

Three methods were compared for maximum lipofuscin extraction. The first two methods (Tappel 1975; MacArthur and Sohal 1982) were specifically developed for lipofuscin extraction and employed chloroform:methanol (2:1) as the extractive solvent; they differ in the optimal volume-to-weight ratio (30:1 and 20:1, respectively), temperature of extraction, and number of times the chloroform phase is washed with water. The third method was developed for lipid extraction in fishes (Bligh and Dyer 1959) and uses chloroform:methanol:water (1:2:0.8) as the extractive solvent. Subsamples ($n = 3$) of cerebellum of *Stenella* sp. collected at the eastern tropical Pacific and kept at −30°C were defrosted, dried with lint-free paper, weighed, and extracted following the three methods as described originally.

Tissues from Dover sole were extracted basically following the MacArthur and Sohal (1982) technique, with two additional steps to ensure a complete washing out of flavoproteins and photooxidation of retinol when present (Fletcher et al. 1973). Tissue was freeze dried prior to analysis. Ten mL of chloroform:methanol (2:1, v/v) was added to a homogenizer containing the sample for a final solvent:sample ratio of about 120:1 (vol/dry weight). The sample was ground with a teflon pestle attached to an electric drill and later submerged in a 40°C water bath for 1 minute. A 2 mL subsample was taken from the homogenate. Three mL of deionized water was added, the sample was shaken, and the emulsion centrifuged 10 minutes at 1,912 *g* and 0°C. After centrifugation, the hyperphase was decanted and a second rinse performed. After decanting the hyperphase a second time, 1 mL of the hypophase (chloroform containing lipofuscin) was sampled and transferred to a polypropylene tube. Three mL of chloroform were added to the sample (for a total of 4 mL) which was then exposed to UV irradiation (254 nm) for 1–2 minutes to photooxidize retinol. This last step was routinely performed for liver tissue.

Samples were then transferred to glass tubes, sealed, and kept in the refrigerator until analysis. Sample fluorescence was measured at the emission peak (430–440 nm) in a quartz cuvette with a Perkin Elmer Fluorescence Spectrophotometer[1] Model MFP-44A. The sample was excited at the peak of fluorescence excitation (~360 nm). The intensity of the fluorescent emission (at 430 nm) was normalized to the intensity of the quinine solution standard (1 mg L^{-1} in 1N sulphuric acid) and expressed in fluorescence units.

Lipofuscin in Dover sole is expressed as 1) total lipofuscin content per organ and 2) weight-specific lipofuscin concentration, calculated by dividing the total lipofuscin content by the dry weight of the entire organ.

Lipofuscin from rainbow trout tissues was extracted following the Bligh and Dyer (1959) technique, without modifications. Whole tissues were ground in water with a tissue homogenizer to give a final concentration of 100 mg of tissue (wet weight) in 0.8 mL of homogenate. A sample of 0.8 mL was taken and solvents were added to give a final ratio of 1:2:0.8 (chloroform:methanol:water) with a solvent to sample ratio of 20:1 (vol/w). The sample was then filtered through a 2.4 cm glass fiber filter (Whatman GF/C), the tissue re-extracted with 1 mL of chloroform and refiltered. The extract was then washed with 3 mL of water, shaken, and centrifuged for 10 minutes at 1,912 *g* and 0°C. One mL of the chloroform hypophase was subsampled and fluorescence estimated as described above.

Lipofuscin in rainbow trout is expressed as 1) total lipofuscin content per organ and 2) weight-specific lipofuscin concentration (total lipofuscin content of the organ divided by its wet weight).

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

Efficiency of Extraction

Lipofuscin was successfully extracted and quantified from three different fish tissues: brain, heart, and liver. Wavelengths of fluorescence excitation and emission maxima of extracted lipofuscin in chloroform are presented in Figure 1. All maxima are within the range cited by Sheldahl and Tappel (1973); fluorescence excitation maxima were between 340 and 370 nm and fluorescence emission maxima between 420 and 470 nm.

Retinol (wavelengths of maximum fluorescence excitation at 325–340 nm and maximum fluorescence emission at 475 nm) was photooxidized by exposing the chloroform extract to UV irradiation (254 nm). As expected, retinol was found in liver and sometimes it was present in brain and heart tissues. For example, wavelengths of fluorescence excitation and emission maxima in liver of Dover sole shifted from 352 to 365 nm and from 470 to 440 nm, respectively, after UV irradiation (see Figure 1C). Mullin and Brooks (1988) also found that this UV irradiation is effective in oxidizing retinol although they did not find significant retinol interference in fish tissue. It seems liver tissues may require UV irradiation to oxidize retinol while brain and heart tissue should be checked for retinol presence before irradiation.

The extractive efficiency of the three methods tested are compared in Table 1. All methods extracted similar fluorescent compounds from the brain of *Stenella* sp., as the fluorescence excitation and emission spectra were similar. The MacArthur and Sohal (1982) method extracted significantly more fluorescent pigment, than did either the Tappel (1975) or the Bligh and Dyer (1959) method which extracted 66% and 46% of maximum extraction, respectively). Thus all three methods are useful for quantitative estimation of extractable lipofuscin in fish tissue but

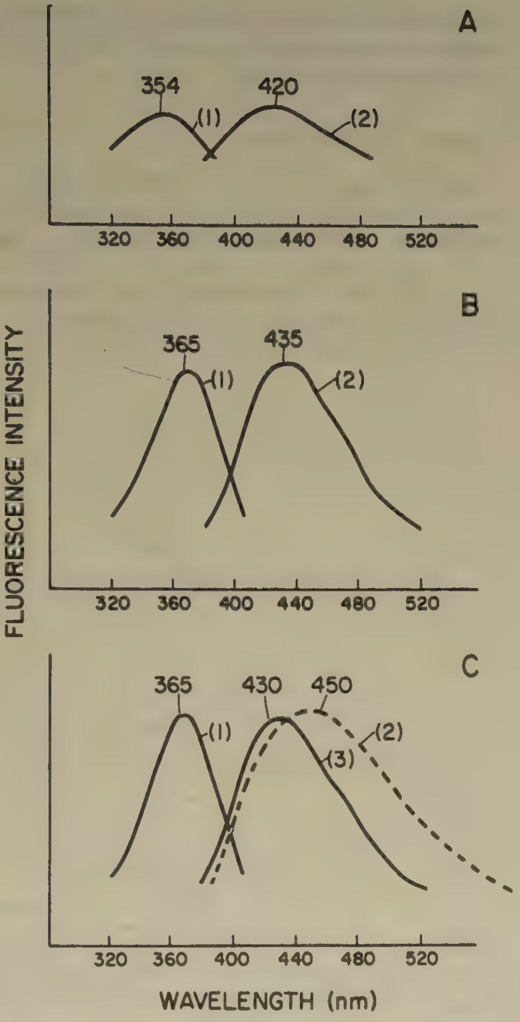

FIGURE 1.—Spectral characteristics of lipofuscin extracted from Dover sole, *Microstomus pacificus*, tissues (uncorrected spectra). In chloroform. (A) Brain: (1) Lipofuscin fluorescence excitation spectrum (emission wavelength 440 nm); (2) lipofuscin fluorescence emission spectrum (excitation wavelength 365 nm). (B) Heart: (1) Lipofuscin excitation spectrum (emission wavelength 430 nm); (2) lipofuscin fluorescence emission spectrum (excitation wavelength 365 nm). (C) Liver: (1) Lipofuscin fluorescence excitation spectrum (emission wavelength 430 nm); (2) lipofuscin emission spectrum (excitation wavelength 365 nm) before UV radiation; (3) Same as (2) after UV radiation (254 nm).

TABLE 1.—Comparison of the three methods of lipofuscin extraction in brain tissue. Fluorescence excitation at 360 nm and fluorescence emission at 440 nm. Results are presented as fluorescence units per mg of wet tissue, where the fluorescence emission signal is normalized to the intensity of emission of a standard quinine sulfate solution (1 mg L^{-1} in 1N sulphuric acid). The three methods were significantly different from each other, $P < 0.05$, Newman-Keuls range test (Zar 1974). ANOVA: F ratio = 21.81, 2 df, $P < 0.05$.

	Fluorescence units			Fluorescence maxima	
	Average 10–3	SD 10–3	*n*	Excitation (nm)	Emission (nm)
MacArthur and Sohal (1982)	4.30	0.39	3	362	445
Tappel (1975)	2.83	0.37	3	362	440
Bligh and Dyer (1959)	1.98	0.45	3	360	445

comparisons of amount of concentrations between tissues or species cannot be made if different extraction methods are used.

Lipofuscin Concentration

The total concentration of extracted lipofuscin in Dover sole brain tissue was positively correlated with fish length (Fig. 2A) ($Y = -15.4 + 0.516\,X$, $r^2 = 0.43$; $b \neq 0, P < 0.01$, $t = 5.1$, df $= 34$). Furthermore, total extracted lipofuscin content in the brain was positively correlated with age in organisms estimated by annular increments in otoliths to be from 2 to 15 years old (Fig. 3A) ($Y = -2.5 + 1.0\,X$, $r^2 = 0.75$; $b \neq 0$, $P < 0.01$, $t = 5.5$, df $= 10$). On the other hand, in older Dover sole (estimated age from 20 to 45 years; $n = 26$) the total extracted lipofuscin in the brain did not increase with their estimated age. The concentration of lipofuscin in the brain (extracted lipofuscin concentration per unit of g dry weight) followed a similar pattern (Fig. 3B). The concentration in the brain increased linearly with age for fish 2–15 years old ($Y = 30.39 + 14.85\,X$, $r^2 = 0.79$, $b \neq 0$, $P < 0.01$, $t = 6.66$, df $= 10$) but fishes older than 15 years did not show an increase in pigment concentration with age.

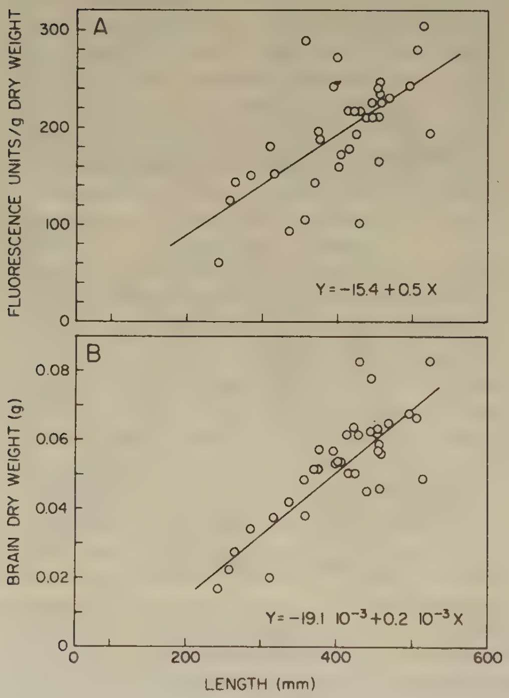

FIGURE 2.—Dover sole, *Microstomus pacificus*, brain: (A) Extracted lipofuscin per unit of dry weight as a function of fish length (mm) (n = 36); (B) brain dry weight (g) as a function of fish length (mm). Fluorescence units: the intensity of fluorescence normalized to a standard solution of quinine sulfate (1 mg L^{-1} in 1N sulphuric acid).

The total extracted lipofuscin content extracted from rainbow trout brains increased with age (Fig. 4A) ($Y = 0.14 + 0.18\ X$, $r^2 = 0.37$; $b \neq 0$, $P < 0.01$, $t = 3.75$, df $= 23$), as did the content of the heart (Fig. 4C) ($Y = -0.54 + 0.82\ X$, $r^2 = 0.67$; $b \neq 0$, $P < 0.01$, $t = 7.36$, df $= 23$), and liver (Fig. 4E) ($Y = -2.86 + 5.81\ X$, $r^2 = 0.62$; $b \neq 0$, $P < 0.01$, $t = 7.54$, df $= 34$) from 3 months to 3 years. The concentration of extracted lipofuscin per unit wet weight of heart tissue did not change with age (Fig. 4D) whereas that of brain and liver tissue decreased with age (Fig. 4B, F).

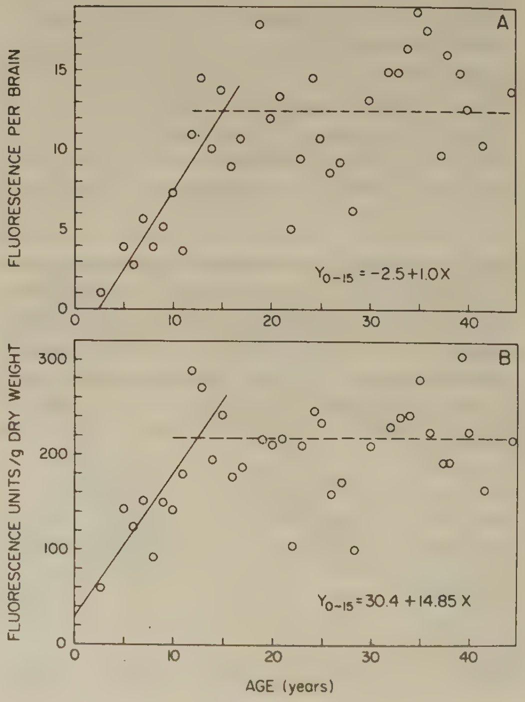

FIGURE 3.—Lipofuscin in Dover sole, *Microstomus pacificus*, brain tissue as a function of age ($n = 36$). (A) Total lipofuscin content per brain; (B) weight-specific (g dry weight) lipofuscin in brain.

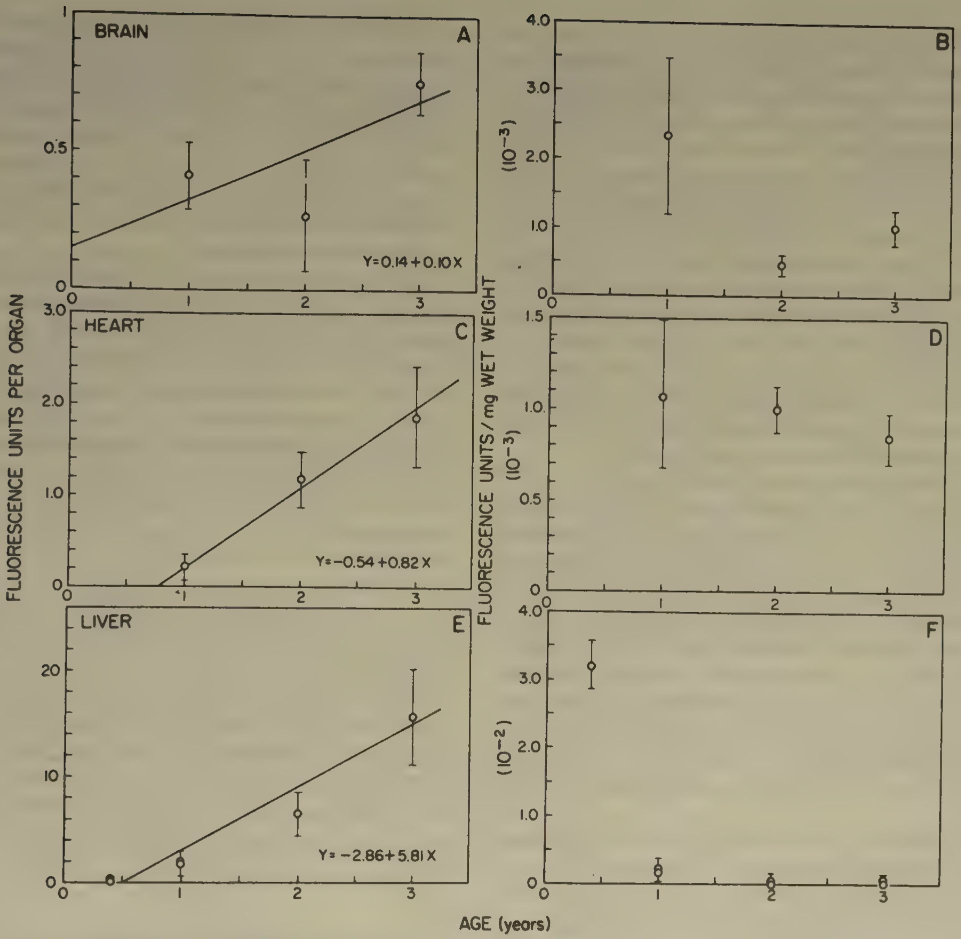

FIGURE 4.—Lipofuscin in rainbow trout, *Salmo gairdneri*, as a function of age ($n = 21$). (A) Total lipofuscin in brain; (B) weight-specific (mg wet weight) lipofuscin in brain; (C) total lipofuscin in heart; (D) weight-specific (mg wet weight) lipofuscin in heart; (E) total lipofuscin in liver; (F) weight-specific (mg wet weight) lipofuscin in liver.

Discussion

Our results indicate that lipofuscin accumulated in the brain of Dover sole with time (Fig. 2A). The concentration of lipofuscin increased over a wide range of fish lengths and with estimated age of 15 years but did not increase with older fish. Several explanations exist for the lack of change in concentration in older fish: 1) older fish were incorrectly aged; 2) growth of brain tissue masked the actual rate of accumulation; and 3) the rate of accumulation changed during the lifespan of this species due to changes in metabolic activity. Either one or several of these factors may cause the lack of lipofuscin accumulation in older fish. We consider each of these issues below.

We do not know the accuracy of the age determination in Dover sole but believe it is unlikely that 3 readers would confuse fish aged 30–40 years with those of 20 years. Although future research will shed more light on this controversial subject, we think that grossly inaccurate age determination is the least likely an explanation.

A key difference between fishes and other organisms in which lipofuscin accumulation has been clearly documented as a function of chronological age (mammals and invertebrates) is that fishes have indeterminate growth. For example, Figure 3B indicates that the brain of Dover sole continues to grow long after this fish begins reproduction (450 mm). Thus, unlike mammals and invertebrates which have determinate growth, the total content of extractable lipofuscin in any fish organ cannot be used as a measure of age but rather concentration (content per unit of weight) must be used. Furthermore, even the concentration of lipofuscin in the brain, a slow growing tissue, is a function of both the rate of lipofuscin accumulation and the rate of tissue growth. It follows then, that if the rate of brain growth is such that it masks the actual rate of lipofuscin accumulation in older organisms, lipofuscin concentration will not increase with time.

A critical assumption underlying the use of lipofuscin as a determinant of age is that metabolic rate, and hence lipofuscin accumulation rate, remains fairly constant over the portion of the life history of interest. The rainbow trout were reared in a hatchery where no net change in the environment occurred from 1983 to 1985. Dover sole, on the other hand, gradually migrate into deeper, colder, and less oxygenated waters as they age. Presumably the metabolism of fish under these conditions would be lower as might be the rate of lipofuscin accumulation in the brain.

The literature on fishes provide no conclusive evidence that lipofuscin is an accurate index of age over the entire lifespan. Hill and Radtke (in press) reported that the extracted lipofuscin per unit dry weight in the brain of the tropical fish *Dascillus albisella* accumulates exponentially with age. The relationship is driven by a single point for an 11-year-old individual and it would probably be linear without that single point, if only fish 1–7 years old were considered. In hatchery-reared *Cyprinus carpio* the total extracted lipofuscin per unit of dry weight in the brain of fish of the same age (6 years) increased with weight over 8-fold range in weight (Griven et al.[2]). About 45% of the lipofuscin content could be explained by difference in weight among fish. Thus, in fish of the same age there was a strong size effect on lipofuscin concentration. These results are very similar to those found in this study. Aloj Totaro et al. (1985) found that lipofuscin increased over a range of 0–2 years. But the method was different as they measured lipofuscin granules present in the electric lobe of *Torpedo marmorata* brains rather than using extractable lipofuscin of the entire brain. Thus, all studies to date seem to indicate that accumulation occurs in the brains of fishes, but results are not conclusive owing to small sample sizes, limited age ranges, and failure to identify the effects of brain growth on rates of accumulation.

Additional research is required to evaluate lipofuscin as a method of age determination in fishes. The effect of brain growth on lipofuscin accumulation rates must be considered in such studies. A promising approach in this regard may be to estimate lipofuscin on a per cell basis instead of on a weight basis. This could be accomplished by either expressing extracted lipofuscin relative to DNA concentration or by histological techniques.

Acknowledgments

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ESTIMATION OF NATURAL MORTALITY IN FISH STOCKS: A REVIEW

E. F. VETTER[1]

ABSTRACT

The instantaneous rate of natural mortality (*M*) is an important but poorly quantified parameter in most mathematical models of fish stock dynamics. This report reviews methods used commonly to estimate *M* for fish stocks, sensitivity of some common fishery models to values chosen for *M*, and evidence refuting the common assumption that a constant value can be an adequate approximation of *M* within single stocks.

With the exception of simple surplus production models (e.g., Schaefer 1954; Pella and Tomlinson 1969) all mathematical models of fish stock dynamics include as a parameter the instantaneous rate of natural mortality (*M*). The models do not require explicitly any particular form for *M*; it can be constant or can vary in any imaginable form. But because natural mortality has proved extremely difficult to measure directly, *M* is assumed almost universally to be some constant specific to whatever stock is being modeled. This is particularly true for analyses of commercial fish stocks, which often require estimates of *M* only for the postrecruit ages. Decreases in natural mortality with increasing age during egg and postlarval stages are so dramatic compared to apparent changes during postrecruitment ages (e.g., Cushing 1975) or compared to differences between different sexes, collection sites, seasons, years, cohorts, or stocks within species, that variations in *M* during these later (postrecruitment) ages are often assumed negligible.

Whether this assumption is in fact acceptable is the subject of this report. The answer is no, it is probably not acceptable in most cases. That answer follows from the information presented in Sections II through V, with the following conclusions:

Section II: Current methods for estimating natural mortality: a review of methods used currently to estimate *M* in fish populations. All of these methods have strong limitations or disadvantages.

Section III: Sensitivity of fishery models to choices for *M*: a review of the sensitivity of some standard fishery models to different choices for input value(s) of *M*. Existing studies show that the models are sensitive and that sensitivity is affected not only by the values chosen for *M*, but also by interactions between *M* and the values chosen for other parameters in the models.

Section IV: Evidence for nonconstant *M*; factors influencing death rate: a review of factors assumed or shown to affect *M* in fish stocks. Available information implies that many such factors exist, acting alone or in concert.

Section V: Evidence for nonconstant *M*; variability within and between groups: a review of existing quantitative evidence for the extent of variability in *M* between but especially *within* stocks. Because almost all fishery models focus on single stocks, variability within stocks (as opposed to between stocks) is the most important question. Some studies show strong differences between mortality rates of various groups of fish; some do not. Those which do not have tended to assume there would be none, and have often used catch curve regression analysis to derive a single estimate from data combined over many groups (usually years) of data. The few studies from which it is possible to determine ranges of estimates show differences of at least 50 to 100% between minimum and maximum estimates for single groups (e.g., stocks) of fish.

The report's major conlcusions are that natural mortality is far from constant for many fish stocks, and that this variability is extensive enough that it should not be ignored. Analyses of

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fish stock dynamics need much more rigorous estimates of **within-stock** variability (both trends and variance) in *M* for exploited fish stocks.

II. CURRENT METHODS FOR ESTIMATING NATURAL MORTALITY

Three methods are used currently or have been proposed to estimate *M* in fish populations: 1) analysis of catch data, usually from commercial fisheries but also from sampling programs specifically conducted for stock assessment (this includes mark-recapture studies), 2) correlations of *M* with other life history parameters, and 3) estimation of deaths due to predation. I describe below each method in turn, listing both advantages and disadvantages of each.

Catch-Analysis Methods

Methods for deriving estimates of natural mortality from catch data are based on measuring decreases in abundance, either relative or absolute, in groups of fish during two or more successive periods of time. Groups may be distinguished on the basis of any identifiable characteristic, e.g., size (length or weight), age, sex, location and time of capture, or some identifiable tag or mark.

The most common grouping is by age, for two reasons. First, age has been considered historically the most important factor potentially affecting estimates of mortality rate and subsequent results from the most commonly used fishery models (e.g., Heincke 1913; Baranov 1918). This is probably because the methods were developed for temperate water fisheries which tend to have obvious annual reproductive cycles, so that individual year classes are often relatively easy to distinguish. Second, the earliest method of estimating *M* (catch curve analysis, discussed below) depends on determining the rate during successive ages.

Regardless of the grouping criterion, methods for estimating *M* use generally one of two types of data. The first type is simply subsamples of unmarked catch. These subsamples contain fish selected randomly and classified into groups on the basis of size (length or weight). The second type is mark-recaptures, in which previously marked individual fish can be identified and classified after recapture into groups on the basis of this positive identification. Estimates of mortality are usually derived from samples of unmarked fish by analysis of resulting "catch curves" (Ricker 1975). Because it has been used so frequently, catch curve analysis is discussed below in some detail.

With marking it is possible to follow the history of individual fish, so many different types of estimation procedures exist for deriving estimates of mortality from mark-recapture data (e.g., Ricker 1975; Jones 1979; Brownie et al. 1985). Because so many variations are possible, marking experiments are discussed only generally, stressing the basic advantages and disadvantages of marking data relative to data from unmarked samples, in deriving estimates of mortality from these data.

Size-frequency distributions from unmarked subsamples of catch (the first type of data) are converted usually to age-frequency distributions, on the basis of previously determined relationships between age and length or age and weight. Subsequent analyses concentrate on analyzing this resulting curve of age-composition (e.g., Ricker 1975). Abundance usually decreases exponentially with size (or age) in this type of sample. Converting the abundances to their logarithmic values often results in a relatively linear decrease during most exploited ages (or sizes), after some initial increase in vulnerability. Graphs of these logged-frequency distributions are usually called "catch curves", and their analysis, "catch curve analysis". "Catch curve analysis" generally consists of determining the best-fit straight line through the decreasing portion of the logged-frequency distribution, because if the decrease in abundance is truly exponential, the slope of this line through the log-transformed data is the instantaneous rate of decrease in abundance (e.g., Ricker 1975).

There are two basic types of catch curves, distinguished on the basis of when the data were collected and how many groups are represented in the curves. The first, horizontal catch curves, includes data from several groups (e.g., size or age classes) collected at a single point in time (or combined from two or more points in time). Thus, horizontal catch curves reflect "ancient history". The individuals contributing to the frequency distribution were not originally all members of the same group. To use this type of catch curve, one must assume that for each successive age, risk of mortality has been historically the same for all individuals achieving that age. If this has not been the case, the catch curves may show various types of curvature in the descending leg, but absence of curvature is no guarantee that the rates have in fact been constant.

Thus, horizontal curves are subject to the extremely restrictive assumption that the groups from which the data were collected must be in steady state relative to each other, i.e., their relative abundances must be constant through time. If this is true, then a graph of data collected at a single point in time, which may include, for example, individuals from 5 consecutive year classes displayed as frequencies at 5 consecutive ages, will look the same as the 5 graphs of data that will result from collecting samples during 5 consecutive years (ages) from each of the 5 year classes. If these conditions are not met, simple linear fitting to determine a single estimate for mortality will be inappropriate.

The second type of catch curve, longitudinal, includes data collected from a single identifiable group over a protracted period of time. Most often, this will be a single cohort of fish such as single year class, sampled during successive years. Longitudinal curves are not subject to the assumption of steady state, but do share with horizontal catch curves several other severe disadvantages. These include 1) groups must be adequately identifiable; 2) groups must be closed to migration, so that changes in abundance are due only to fishing or natural mortality, or if migration does occur, it must occur in proportion to the age distributions in the local groups; 3) samples must represent adequately the true composition of the groups in nature; 4) rate(s) of mortality must be relatively constant between groups over time, so that the log-transformed frequency distributions are truly linear (e.g., Jensen 1984); 5) compensatory relationships between stock levels and natural mortality, or fishing mortality and natural mortality, must not be present.

Methods for estimating *M*, which assume to greater or lesser degrees that the conditions listed above are met, have been described repeatedly. The methods tend to fall into two categories. Methods in the first category estimate *M* from catch records of unexploited or lightly exploited groups of fish. In these groups, *F* equals or approximates zero. Therefore, the observed rate of decrease (*Z*) equals or approximates *M*, because *Z* equals the sum of *F* and *M* (e.g., Heincke 1913; Baranov 1918; Ricker 1947; Beverton and Holt 1957; Robson and Chapman 1961; Pauly 1982; Munro 1982; and among others).

Methods in the second category estimate *M* by determining *Z* at various levels of fishing effort, then using the observed relationship between *Z* and effort to predict, via regression analysis or manipulation of various ratios, the value of *Z* at zero effort (e.g., Silliman 1943; Beverton and Holt 1957; Paloheimo 1961; Lander 1962; Chapman and Murphy 1965; Paulik and Robson 1969; Gulland 1983; Butler and MacDonald 1979; Fournier and Archibald 1982; Caddy 1984; and others).

These methods are most appropriate for analyzing catches of unmarked fish. Accurate results depend strongly on accurate measures of catch per unit effort (CPUE) and constant catchability (*q*) because if these conditions (in addition to those listed above) are not met, observed relationships between abundances in different sample groups may not reflect true differences between groups in situ.

Marked fish present fewer problems. Advantages include 1) concentration on measuring relative rather than absolute differences between abundances of different groups, 2) immigration need not be considered, as entire original groups are known to carry marks, and 3) with sufficiently large samples, it becomes possible to test for differences in mortality rate between different groups (e.g., between ages, between sexes, or between sampling sites), rather than having to assume that such effects are negligible.

Reviews and descriptions of various mark-recapture methods appear in papers by Seber (1973), Ricker (1975), Jones (1979), and Brownie et al. (1985). Some of the newer types of marking analyses can solve many of the most vexing problems associated with traditional catch curve analysis (e.g., Reed and Davies 1980; Hochbaum and Walters 1984; Burnham and Andersen 1984; Burnham et al. 1984; Brownie et al. 1985).

Several disadvantages unique to marking operations counteract these advantages, however, even with the newer methods. These disadvantages include various types of mark-induced effects on mortality rates, behavior, and vulnerability to capture, as well as mark loss, unrepresentative mixing of marked fish with their original groups prior to recapture (e.g., Ricker 1975), and especially in commercial fisheries, underreporting or incorrect reporting of recaptures.

Both analysis of catch curves from unmarked fish and analysis of mark-recapture data have the advantage of requiring only catch (and usually effort) data, and these data can generally be collected by sampling catches from commercial fisheries. However, in addition to problems specific to each method, they have in common one or more other major disadvantages: 1) inability to distinguish between losses (or gains) from migration or recruitment versus losses due to fishing or natural causes, 2) imprecision in the estimates of *M* obtained (e.g., Beverton and Holt 1957; Taylor 1958; Bishop 1959; Paloheimo and Dickie 1966; Ricker 1975, 1977; Doubleday 1976; Pauly 1980; Larkin and Gazey 1982; Paloheimo 1980, 1982; Myers and Doyle 1983; Roff 1984), 3) sensitivity to size-specific mortality affecting the estimated age-structure of the group (Ricker 1969), 4) errors in estimates of age, such that abundances-at-age derived from age-length conversions are unrepresentative, 5) where analyses are conducted on data combined over two or more cohorts, the unlikely condition that mortality rates were in fact similar for all cohorts, and 6) problems inherent in the analyses themselves (e.g., Barlow 1984). Disadvantages 1, 4, and 5 may not apply to marked fish. Disadvantage 5 does not apply to single cohorts. But collections from marked groups and single cohorts are still vulnerable to the other problems.

Further, although in principle it would be possible to estimate *M* for different ages, times, or places, most commonly in practice a single, fishery-wide constant *M* is estimated by pooling data from throughout the fishery. By implication, the analyst is assuming that the exploited stock was more or less in steady-state over all times and areas of catch so that *M* was relatively constant while that data set was collected and while (historically) the observed age-distributions were being created. In fact, substantial evidence exists that *M* is not constant, either within a single stock over time (age) or between stocks of a given species in different areas (Sections IV and V).

A final disadvantage is that catch-curve analyses are fundamentally unmechanistic, generated simply by charting changes in abundance. Catch-curve analyses cannot predict the effect of changes in factors that control *M*; thus there is little hope of predicting *M* in the future should conditions change.

Life History Methods

A second approach to estimating the instantaneous rate of natural mortality in fish stocks is based on the observation that *M* often correlates strongly with life history parameters, such as growth rate, age at sexual maturity, costs of reproduction, and maximum age (Table 1).

Typically in such studies, analytical formulas are derived from theoretical relationships between the various parameters (e.g., Beverton 1964), or empirical formulas are derived from regression of *M* against one or more of the parameters (e.g., Hoenig 1983). These models have two significant advantages: 1) they require minimal amounts of data, and 2) they are useful in demonstrating broad trends across species and in developing ecological theory. But because they produce only a single and often very imprecise estimate of *M* for any given group of fish, they are not particularly effective for generating precise estimates of natural mortality or for determining the existence or extent of trends and variability in *M* for given stocks. They will also be no better than the methods used to estimate the values of *M* used in the regressions.

TABLE 1.—Studies relating instantaneous rate of natural mortality to life history traits in fish.

Traits	Species	Source
[1]T_{max}, [2]k, [3]L_{inf}, metabolic rate, reproduction	Various	Beverton and Holt 1959
T_{max}, k, L_{inf}, [4]L_{asm}, fishing	clupeids, engraulids	Beverton 1963
[5]W_{inf}	general	Ursin 1967
T_{max}, [6]$T_{max.biomass}$, k,	general	Alverson and Carney 1975
growth rate	young fish	Ware 1975
L_{asm}, gonad size, condition factor	gadoids	Jones and Johnston 1977
T_{max}	general	Blinov 1977
gonad/body weight index, [7]ASM, T_{max}, L_{inf}	general	Gunderson 1980
W_{inf}, L_{inf}, k, water temperature	175 stocks	Pauly 1980
energy cost of reproduction	general	Myers and Doyle 1983
T_{max}	various	Hoenig 1983
weight	various	Peterson and Wroblewski 1983
k, L_{inf}, L_{asm}	various	Roff 1986

[1] Maximum age,
[2] Von Bertalanffy growth parameter.
[3] Maximum length.
[4] Length at age of sexual maturity.
[5] Maximum weight.
[6] Age at occurrence of cohort's max biomass.
[7] Age of sexual maturity.

Predation Methods

A third class of estimators extends single species cohort analysis to a multispecies assemblage incorporating the major predators and alternative prey of the stock in question. Single species cohort analysis is used to estimate population abundances and annual values for the instantaneous rate of fishing mortality (F) for single groups, usually year classes, of fish (e.g., Pope 1972; Ricker 1975; Gulland 1983). The multispecies extension simply combines cohort analyses for several species (e.g., Anderson and Ursin 1977). The methods all generate estimates of M as the sum of some constant rate of nonpredatory, nonfishing mortality plus the total estimated flux of prey (stock) to each of the major predators. This feeding flux to predators is estimated by first using cohort analyses to reconstruct population sizes of the various groups of predator and prey, then combining these population sizes with observed growth rates for the predators and with estimated preferences for various prey. Thus it becomes possible to estimate the predatory component of M.

Versions of the method have been described by Anderson and Ursin (1977), Majkowski (1981), and Pope and Knights (1982). Applications in a marine system (North Sea) have been described by Anderson and Ursin (1977), in an ecosystem context, by Laevastu et al. (1982) and in lake systems by Forney (1977) and Stein et al. (1981).

The predation method has been developed primarily from analyses of marine systems, especially the North Sea, and much of the literature exists only as "mimeos" or notes associated with ICES (International Council for the Exploration of the Seas) activities. The most readily available discussion of this approach appeared in Mercer (1982), which includes a critical review and discussion by Ursin (1982) of the various methods. Several other discussions appear in Pauly and Murphy's (1982) volume of collected papers from a symposium on theory and management of tropical fisheries. Most of these papers specifically address tropical multispecies systems, but the concepts are broadly applicable. References to other, often less accessible, works can be found in these two general references.

The predation method is elegant in concept but often difficult to apply. Studies by Forney (1977) and Stein (1981) had the distinct advantages of limited species numbers in a small system, and direct quantification of stomach contents. Yet even in lake systems, the sampling problems of estimating Z, population abundances, and so forth, remain often as intractable as in large marine systems. The two greatest problems are 1) the difficulty in defining vulnerability and preference functions for the various prey stocks (e.g., Ursin 1982) and 2) the need to include cohort analyses of all the major interacting species, some or many of which may not be available commercially (and for which therefore data will be scarce).

Despite these problems the approach can certainly generate, for stocks that suffer heavy predatory mortality from other fished stocks, more realistic estimates of M than approaches that simply generate a globally fixed and invariant M. More importantly (and in contrast to the age-frequency or life history methods) the predation method has the advantage of being mechanistic. Predation-related causes and consequences of age, size, site, stock, geographic, or time trends in M can be investigated via perturbation and sensitivity analysis in computer simulation studies or, alternatively, investigated through analysis of existing catch data. It becomes possible (not necessarily feasible) to investigate the implications of varying age or abundance structures of interacting fishery resources.

Thus the predation approach has considerable conceptual appeal for fairly simple systems in which 1) predation is the major force controlling prey abundance, 2) predators have few alternative prey, 3) the possibility can be ignored that predators prefer moribund prey which were about to die anyway, and 4) all major species of predator and prey are sought commercially so that data on abundances and feeding preferences are or can be made available.

Unfortunately, the number of systems satisfying these requirements appears to be fairly small, and of course where predation is a relatively small fraction of M, the multispecies predation method will be particularly ineffective.

III. SENSITIVITY OF FISHERY MODELS TO CHOICES FOR *M*

Although catch-analysis, life history, and predation methods all exist currently for estimating M in fish stocks, in practice the only method used extensively is the first—direct estimation of M from analysis of catch structure. Thus the discussion below of model sensitivity to M is based on this type of estimate. The conclusions reached are not specific to this one method. Model sensitivity to a given derived value of M will be the same, regardless of the method used to derive the value.

General Patterns

Sensitivity analyses of M in fishery models have evolved through two phases. Earlier studies noted the influence of M on estimates of maximum yield ($Y_{\max}$) or maximum yield per recruit ($(Y/R)_{\max}$), and on $F_{\max}$ (the fishing pressure required to produce maximum yield) in Beverton-Holt yield models (Beverton and Holt 1957; Hennemuth 1961; Francis 1974; Parks 1977; Bartoo and Coan 1979; Bulgakova and Efimov 1982). More recently, as cohort analyses have become more popular, more attention has been directed toward assessing the influence of M on age-specific estimates of stock sizes (N_i) and fishing mortalities (F_i) produced by these models (Murphy 1965; Pope 1971; Ricker 1971; Agger et al. 1973; Doubleday 1976; Ulltang 1977; Doubleday and Beacham 1982; Pope and Shepard 1982; Sims 1982a, 1982b, 1984). A few other studies have investigated the effect of M on estimates of maximum sustainable yield (MSY) or total biomass (Francis 1976; Deriso 1982; Beddington and Cooke 1983; Tyler et al. 1985).

Most of these studies have used a single, invariant value for M. Model sensitivity is then assessed by comparing model results using some "best" estimate of M, to results using one (or rarely, more) pair(s) of M values some arbitrary percentage above and below the best estimate. Only a few studies exist of the effects of nonconstant M, where M varies in different groups of fish within a given stock. These include Beverton and Holt's (1957) example of density-dependent M in plaice, and several investigations of age-specific M (Parks 1977; Ulltang 1977; Bartoo and Coan 1979; Sandland 1982; Bulgakova and Efimov 1982; Caddy 1984; Tyler et al. 1985).

No study to date has specifically addressed the problems of estimating values of M for a full fishery analysis, leading from cohort analyses (using M to estimate F_i, N_i, and recruitment R) to estimates of yield or yield-per-recruit using the same M(s) and R subsequently in the Beverton-Holt formulas. Also, no study to date has addressed the possibility and consequences of differing patterns of variability in M, although it has been suggested in one case (Ulltang 1977) that random variations will be unimportant if the rate is constant (on average) over the fished ages.

In general, the earlier analyses with yield models assuming a constant M show that *higher* estimates of M lead to 1) **lower** estimates of $Y_{\max}$ or $(Y/R)_{\max}$ (because fewer survive to be caught), 2) *higher* estimates of $F_{\max}$ (you must fish a bit harder to catch a given amount of those left), and 3) **lower** estimates of age at first capture (t_c; because it pays to catch them before they die, rather than waiting for them to grow bigger but less abundant).

Including density-dependence tends to exaggerate these trends, at least for plaice in the North Sea (Beverton and Holt 1957). Including age-structured M in yield models also affects the estimates, but not necessarily in a straightforward manner. As described below in the section on numeric results, change in model output for a given change in M depends not just on the values chosen for M, but also on those chosen for the other parameters. M is not an independent parameter in these models.

Analyses with cohort or virtual population models which assume a constant value for M show that in general the effect of increasing M is to increase estimates of N_i (because the higher M is, the more fish died in addition to those being caught) and to decrease estimates of F_i. The data show only Z, which is the sum of M and F_i. Assuming Z has been constant, a decrease in F_i requires an increase in M. If Z has been variable, the lower F_i may be explained on the basis of higher N_i, a smaller proportion of which (F_i) would account for the observed catch.

The actual effect, particularly on estimates of N_i, is not necessarily that simple. As with yield models, a given change in M does not always produce the same change in model output. The result depends also on values chosen for other parameters; M is not an independent parameter.

In cohort analysis the results (estimates of N_i and F_i) are particularly sensitive to the relative sizes of F and M (i.e., to the exploitation ratio $E = F/(F + M)$). The effect of assuming an incorrect value (or series of values) of M tends to build up as the analysis proceeds backward in time. This is because with every time step backward the catch (C) is inflated by the factor M in order to estimate at that time the size of the entire stock, not just the size of the catch. That is

$$N_i = N_{i+1} + C_i(F_i + M)/F_i \qquad (1)$$

where F_i satisfies the catch equation

$$C_i = N_{i+1} \, (F_i/F_i + M) \, (e^{(F_i+M)t} - 1) \qquad (2)$$

If M is large relative to F (i.e., the exploitation ratio is low), then errors in N_i can increase progressively and become quite large at the younger ages (e.g., Agger et al. 1973; Murphy 1965; Ulltang 1977; Sims 1982a, 1982b, 1984).

Numeric Results

Although general responses of various models can be determined simply by inspection of the analytic models themselves, the quantitative change to expect in the result (output) for a quantified *change* in M (input) is not always immediately obvious. This is because M tends to occur more than once in various formulas. For example, M appears in both the numerator and denominator in the solution to the Beverton-Holt yield equation (Ricker 1975).

$$\begin{aligned} Y = FN_0e^{(-Mr)}W_\infty(1/(M + F) \\ - 3e^{(-kr)}/(M + F + k) \\ + 3e^{(-2kr)}/(M + F + 2k) \\ - e^{(-3kr)}/(M + F + 3k)). \qquad (3) \end{aligned}$$

So, rather than derive analytical expressions (e.g., Sims 1984), I resort below to a simpler approach. Sensitivity of fishery models to changes of given magnitude in M is assessed by comparing percent change reported in model response (output) to percent change in M (input). In cases for vector (age or density-dependent) M, I have merely described the shape of the M-vector. For these different vectors, I report the percent change in the result due to switching from a vector of one shape to a vector of another shape.

Yield Models

At least four studies (Beverton and Holt 1957; Hennemuth 1961; Francis 1974; Bartoo and Coan 1979) have shown that errors in estimates of M propagate into roughly equal errors in estimates of $(Y/R)_{\max}$, but with sign reversed (Table 2). For example, a 10% overestimate in M will lead to approximately 10% underestimate of $(Y/R)_{\max}$. An equally important result is that the actual magnitude of the effect induced depends strongly not just on the error in M, but on the values chosen for the other parameters in the model.

In another study, Beddington and Cooke (1983) used the Beverton-Holt formulation to investigate the influence of M (constant; 0.1 to 0.8 year^{-1}), t_c (0 to 4 years), and K (the von Bertalanffy growth parameter; 0.1 to 0.5 year^{-1}) on MSY (maximum sustainable yield), expressing the result as "MSY as a % of B_0," where B_0 is the initial or recruited biomass. Higher percentages indicate that more of the original biomass is being taken at MSY. Increasing M by a factor of 8 (0.1 to 0.8 year^{-1}) increased MSY/B_0 by a factor of about 4 to 8, depending on the particular values of t_c and K. Again, errors in M produced roughly the same relative error in the result; and again the actual effect of any given change in M de-

TABLE 2.—Sensitivity of estimated maximum yield per recruit ($(Y/R)_{\max}$) to changes in instantaneous rate of natural mortality (M) and other input conditions. Sensitivity of $(Y/R)_{\max}$ and of changes in M are expressed as percentage difference from nominal responses at nominal (best-guess) M. Symbols are: t_c = age-at-first-capture, F = instantaneous rate of fishing mortality, M = nominal value for M. Frances (1974) used an age-structured simulation model. All other citations used standard yield-per-recruit analyses.

Input conditions	% change in M	% change in $(Y/R)_{\max}$	Species	Source
t_c = constant (3.72) F = variable M = 0.10	+50 −50	−20 +30	plaice	Beverton and Holt 1957
t_c = variable F = constant (0.73) M = 0.10	+50 −50	−60 +50	plaice	Beverton and Holt 1957
F = constant (0.95) M = 0.8	+20 −20	−21 +32	yellowfin tuna	Hennemuth 1961
M = 0.8	+10 −10	−14 +16	yellowfin tuna	Francis 1974
M = 0.60	+25	−20	yellowfin tuna	Bartoo and Coan 1979

pended on the values chosen for the other parameters.

Pope and Garrod (1973) present another example of sensitivity in MSY to values chosen for M. They describe briefly the consequences of using an incorrect constant for M of cod stocks when estimating the F required to generate MSY (F_{MSY}). Underestimating M by 50% (assumed $M = 0.1$ year^{-1}; true $M = 0.2$ year^{-1}) leads to a choice of F_{MSY} that is 67% too high. Overestimating M by 50% (assumed $M = 0.3$ year^{-1}, true $M = 0.2$ year^{-1}) underestimated F_{MSY} by 50%.

The simulations described above tested the effects of choosing alternative constant values for M. Choosing a vector alternative can also have significant effects; again, the magnitude of the effect depends on the values chosen for other parameters. Beverton and Holt (1957) showed that incorporating density-dependence in M for plaice decreased $(Y/R)_{\max}$ by 12%, when holding t_c constant at 3.72 years and letting F vary. Conversely, holding F constant and letting t_c vary decreased $(Y/R)_{\max}$ by about 37%.

Age-dependent values for M were compared with age-constant values by Bartoo and Coan (1979), Bulgakova and Efimov (1982), and Tyler et al. (1985). In their analysis of Atlantic yellowfin tuna stocks, Bartoo and Coan found that replacing an assumed constant M of 0.8 year^{-1} with an age-structured M increasing from 0.1 year^{-1} at age 0 to 1.2 year^{-1} at age 7, increased $(Y/R)_{\max}$ by 17% (from 6 to 7 kg).

Estimating total yield (Y_t) rather than (Y/R) and estimating R as a function of constant versus age-specific M in analysis of catch curves for relatively unexploited stocks of Pacific ocean perch and Oregon hake, Bulgakova and Efimov (1982) found that replacing a constant (age-averaged) M with age-variable M tended to increase estimated Y_t when fish recruited fairly late to the fishery, but decreased Y_t if the fish recruited early. This is because of the interaction between the values assumed for M (constant or age-variable) and the value calculated for R from each type of mortality curve.

Starting with a given value for recruitment at age 6 years (from Efimov 1976), they calculated R twice for ages 4 and 8 years—once with age-averaged M and once with age-specific M. Because in this set of data the age-averaged M was generally higher than the age-specific M at the tested ages of recruitment (ages 4, 6, or 8 years), back-calculations with age-averaged (i.e., constant) M predicted fewer recruits than back-calculations with age-specific M. With fewer recruits and generally higher M, potential yield at later ages obviously must drop. Differences in predicted potential yield ranged from about -30% at t_4 (age-specific estimate lower than age-averaged estimate, when fish were assumed to recruit to the fishery at age 4 years) to $+15\%$ at t_6 (age-specific estimate higher) and to $+60\%$ at t_8.

Tyler et al. (1985) tested (among other things) the effects of ignoring "true" age-structure in M and using instead a constant value in estimating stock biomass using Deriso's (1980) delay-difference model. They did the tests on catch data generated by Walter's (1969) age-structured simulation model of cod, using three different (input) age structures for M in Walter's model. After generating "catch data" from Walter's model, they analyzed the simulated data set using Deriso's model with constant M (= 0.5 year^{-1}). The age structures tested were 1) mortality increasing and then decreasing with age (Walter's original mortality vector spanning ages 3 to 12 years; age-averaged $M = 0.55$ year^{-1}, range = 0.33 to 0.70 year^{-1}), 2) mortality increasing with age (ages 7 to 12 years; average $M = 0.5$ year^{-1}, range 0.3 to 0.7 year^{-1}) and 3) mortality decreasing with age (ages 7 to 12 years; average $M = 0.5$ year^{-1}, range 0.7 to 0.3 year^{-1}). In all three cases Deriso's model with constant M misestimated the "true" biomass generated by Walter's model (with age-structured values for M). The differences were relatively small, however: -13% for the increasing and then decreasing series, $+19\%$ for the decreasing series, and $+4\%$ for the increasing series. These differences were due to the differences in M, and not the differences in model structure; generating and analyzing biomass with the same constant M in both models led to a discrepancy of only 0.5%.

By analogy to life history patterns in other adult animals, M (after recruitment into most fished stocks) is more likely to increase with age than to cycle or decrease. By implication, the simulation results from the increasing series are probably most realistic. If so, the effects of ignoring age-structure in favor of using a constant M may be relatively small (5 to 20%), at least for the cod stock simulated in this study. But the results obviously depend again not just on correctly choosing the values for M, but on the values chosen for the other parameters. In this case, Tyler et al.'s (1985) results imply that age-structure in M can be relatively unimportant, at least when the assumed constant is evenly bracketed by the "true" age-structure in M.

Further simulations by Tyler et al. (1985) using a wide range of constant values for M (0.4 to 1.4 year^{-1}) and the growth rate parameter rho (mean Ford growth coefficient for the fishable stock; 0.46 to 1.6) showed that incorrect guesses of M (and rho) could produce errors up to 1,000% in estimated biomass. More realistic ranges for the two parameters (0.4 to 0.8 year^{-1} for M, 0.6 to 1.2 for rho), extending about 50% above and below the "true" values for these parameters, induced much lower error in biomass estimates (about the same order of magnitude, 50 to 100% below and above the "true" biomass). As before, changes (errors) of a given amount in M (expressed as fraction or percentage of the original value) appear to produce about the same amount of change (expressed as percent of original value) in simple estimates of yield, depending on the conditions of other parameters in the model.

Chatwin (1958) compared estimates of $Y_{\max}$ from lingcod populations. Rather than compare constant and age-variable values for M, he assumed several different values for an average (constant) M in adults, but assumed that M increased from the assumed average for adults to higher values in both juveniles and senescent fish. He reports no quantitative results but states, as found above, that increasing the average M, for a given F, considerably decreased $Y_{\max}$, that decreasing M increased $Y_{\max}$, and that size at first capture changed relatively little with those changes in M.

These comparisons between age-structured versus constant M, or between different constants have demonstrated that effects on results can be large for some combinations of parameters yet small for others. Alternative choices drawn from apparently realistic parameter values lead to relatively small differences in estimates of M. Specific amounts of change depend strongly not only on the values chosen for M, but also on the value of M relative to values chosen for the other interacting parameters in the yield models. For most choices of parameter values, sensitivity of output is roughly equal to perturbation of input.

Cohort Analyses

Effects of interactions between changes in M and values chosen for other parameters is even more obvious in stock reconstruction analyses (e.g., cohort analysis and virtual population analysis (VPA)). These analyses are used to "reconstruct" estimates of stock abundance during previous years, based on catch data and assumptions about the value(s) of M during those previous years. Studies of sensitivity to M in Beverton-Holt types of yield or biomass assessments were usually empirical, based on analyses of catch data from specific fisheries. Studies of sensitivity to M in VPA and cohort analysis include both theoretical and empirical studies; i.e., simulations using totally contrived data sets (e.g., Agger et al. 1973), analyses of specific data sets (e.g., Pope 1971; Doubleday and Beacham 1982) and combinations of analytical evaluations and analysis of specific data sets (e.g., Doubleday 1976; Ulltang 1977; Sims 1982a, 1982b, 1984).

Simple analyses of sensitivity to M, in which M is varied but all else is held constant, include 1) Pope's (1972) analysis of Atlantic yellowfin tuna, in which he found that replacing constant M with age-structured M (higher Ms for older fish) produced lower estimates for fishing mortality (F_i) in the later ages, but had little effect on estimates for the younger ages, and 2) Doubleday and Beacham's (1982) statement that 10% error in constant M translated into 9 to 14% error in estimates of R (at age 3) for cod in the Gulf of St. Lawrence.

Somewhat more complicated analyses are presented by Ulltang (1977) and Sims (1982a, 1982b, 1984). Ulltang evaluated the effects on model predictions of F_i and N_i, of several types of variation in M. These included no variation (uniformly constant M), M constant within years but varying randomly between years, M varying with age, and M varying with season. Sims evaluated the effects of choosing various constants for M on estimates of N_i, and derived an analytical expression relating variance in M to expected variance in estimates of abundance.

In Ulltang's simulations, increasing (decreasing) a constant M by 50% (from 0.2) decreased (increased) F by about 20% ("true" F's ranging from 0.4 to 0.8). Creating a data set with M varying randomly from one year to the next, then analyzing those data with an assumed constant M, Ulltang (1977) found that the Z calculated from the constant-M model was on average the same as the "true" Z from the random-M model. He concluded that random fluctuations in M will cancel out during analysis and so can be ignored. Ulltang assessed the influence of age-dependent M compared with constant M by generating a catch curve with age-variable M (decreasing curvilinearly from 0.3 at age 1 to 0.1 at age 10, average about 0.2) and F equal to 0.2, then analyzing the catch with F equal to 0.2 or 0.6, and M equal either to 0.1 or 0.2. Choice of M made little difference in estimates of stock size for the case of high F (0.6), because most of the deaths were due to (observed) fishing. When F was low (0.2), stock-size estimates were much more sensitive to incorrect choices for M, because most of the deaths were due in this case to M, which was unmeasured and therefore unobserved.

Ulltang (1977) simulated seasonal changes in M by concentrating all deaths in either the first or last quarter of a year. Estimated stock sizes (N_i) changed relatively little; with $F = 1.2$ and $M = 0.4$, N_i was a maximum of 10% higher if all deaths occurred first quarter, 10% lower if all occurred in the last quarter.

A serious problem with the conclusions reached by Ulltang (1977) is also common to all the other studies discussed above; they are based on relatively few combinations of values for the various parameters, and relatively few simulations. For example, the conclusion that random errors in M will tend to even out is intuitively attractive, provided the time scale of variation is short relative to the generation time of the fish. In fact random variation in M did even out in the two sets of simulations he conducted. But the examples he chose included only one set of ages (2 to 10 years), with relatively high values of F (0.5 to 0.8 year^{-1}) compared to the values tested for M (0.1, 0.3 year^{-1}). The gravity of consequences from choosing an incorrect M depends very heavily on the size of M relative to the size of F, i.e., on E. Had he chosen different values for his simulations, he might have reached very different conclusions. This is probably the basis for the discrepancy between Ulltang's conclusion that seasonal effects are minor, versus Sims' (1984) conclusion that seasonal effects can be quite large, if M is high.

Sims (1984) attempted to overcome this problem (trying to draw general conclusions from the results of simulations based on particular, or relatively few, sets of parameters) by analytically deriving formulas for relative error in stock-size estimates, and then testing the formulas with data from actual fisheries. He used this approach twice: once to assess the effects of seasonality (Sims 1982a) and once to consider in general the effects of different choices (errors) for constant M (Sims 1984). But his results (and equations for error) show clearly that error in estimated stock sizes depends on several parameters and that the effects of one can be strongly dependent on the values chosen for the others. Choosing a high M (0.6 year^{-1}) and concentrating catch during the first quarter of the year overestimated R by 20%; concentrating catch during the last quarter underestimated R by 23% (compared with the 10% error found by Ulltang).

Within the same analysis, reducing M by half (to 0.3 year^{-1}) reduced the error in R by half, but the same reduction of error in R was also achieved by leaving M high and reducing F. In assessing specifically the effects of error in M on error in R, Sims (1984) showed very different effects on estimates of R in heavily fished versus lightly fished cohorts of Atlantic bluefin tuna. Changing M by 50% led to changes in estimated R of 60 to 260% in the lightly fished cohort, but only to relatively smaller changes of 35 to 70% in the heavily fished cohort. Again, the magnitude of the error in model predictions depended not just on the magnitude of M, but on its relationship to the other parameters in the catch equation, particularly F.

Errors (expressed as percentage change in output for a given change in input) in model output in the simulations described above, all of which tried to use apparently realistic values for model parameters, rarely exceeded 50%, and were often less than the error introduced into values chosen for M. By implication, the effects of incorrectly guessing M may be relatively unimportant if M is relatively small (e.g., in this situation not more than about 0.5 year^{-1}) and relatively invariant, although the actual magnitude of effect due to any given percentage change in M depends on the values chosen for other parameters.

So, inaccurate estimates of M might be important or they might not. It all depends on the magnitude and variability of M within a given stock (or group). Although untested, it seems likely that estimates of M for groups in which M varies little and is relatively low, are more likely to be reasonably accurate than estimates of M from groups in which M is large and variable. The following section reviews evidence that M does in fact vary both within and between groups of fish, and the succeeding section reviews evidence for the magnitude of that variability in ostensibly similar groups.

IV. FACTORS INFLUENCING DEATH RATE

Despite the fact that in most fishery models, M is assumed to be constant for all exploited ages in any given stock, abundant evidence exists to the contrary. Natural mortality has been shown to vary with age, density, disease, parasites, food supply, predator abundance, water temperature, fishing pressure, sex, and size. Evidence for relationships between these factors and M, and selected references for each, are presented below.

Changes in mortality rate with **age**, within single groups of fish, have been demonstrated and discussed more frequently than changes with any other factor. References include, among others, Baranov (1918, plaice), Sette (1943, Atlantic mackerel), Ricker (1945, 1947, lake fish; 1969, 1975, various species), Beverton and Holt (1959, many species of marine fish), Beverton (1963, engraulids and clupeids), Boiko (1964, sturgeon), Cushing (1975, plaice), Blinov (1977, fish in general), Bulgakova and Efimov (1982, Oregon hake and sea perch), Sandland (1982, fish in general), Smith (1985, clupeoids), Roff (1986, fish in general). Evidence for changes with senescence for fish in general has been discussed or documented by, among others, Woodhead (1979) and Craig (1984).

Although specific patterns vary with species (e.g., Woodhead 1979), in general M is extremely high during egg and larval stages (e.g., 2 to 10% per day in plaice and clupeoids (Cushing 1975; Smith 1985)), falls precipitously during the juvenile period, becomes relatively stable during intermediate adult ages and increases again with senescence. But even during these relatively stable mid-adult ages, changes in M with age can be substantial, particularly in short-lived fish (e.g., Ricker 1947, stunted versus "normal" whitefish).

Changes in natural mortality rate with **size** (rather than age) within single groups of fish (usually stocks), have been discussed by Baranov (1918, plaice), Ricker (1969, size-selective mortality in general), Ware (1975, larval fish), and Peterson and Wroblewski (1984, many species). Differences in natural mortality rate between populations of the same species in different environments, or even in different areas of a single environment (e.g., a single lake) are documented by Ricker (1947), Kennedy (1954), and Schupp (1978). Year-to-year differences in natural mortality rates of single stocks from a given area are shown by Pope and Knights (1982, plaice) and by Henderson et al. (1983, whitefish). Density-dependent changes in M are discussed by Beverton and Holt (1957), Cushing (1967), Tyler and Gallucci (1980), Backiel and LeCren (1978), Jones (1982), and others. Differences in M between sexes have been documented by Beverton and Holt (1957, plaice), Ricker (1947, rock bass), and others. Changes in natural mortality rate related to the cost of reproduction have been discussed by Jones and Johnston (1977), Roff (1984), and others.

Other factors that affect M either alone or in combination with other factors include disease and parasitism (reviewed by Lester 1984), starvation (Hewitt et al. 1985; Theilacker 1986: larval anchovy), physiological state (Smith 1985), and fishing pressure (Ursin 1982; Munro 1982). Additional examples are cited by Beverton and Holt (1957), Anderson and Ursin (1977), Sissenwine (1984), and Hunter (1984).

Most of the factors listed above (e.g., age, size, sex) are indirect influences on M. The most important factor directly affecting natural mortality rate is probably predation; this is implied by a large body of literature describing changes in prey community composition and abundance following changes in composition and abundance of predators (e.g., Carpenter et al. 1985).

Direct evidence that predators account for most natural mortality in fish stocks is difficult to gather (Section II). To quantify the fraction of M due to predation, one must know, not only relative changes in abundance, but absolute population density of all predators and prey together with consumption rates and prey preferences of all the predators. Although this is rarely possible, at least two studies from freshwater systems do present quantified estimates of predatory mortality in relation to available prey. Forney (1977) quantified predation mortality in a relatively simple, unmanipulated lake system where there were few species of predator and prey. Combining stomach-content estimates of prey consumed with trawl-sample estimates of predator and prey abundance, he concluded that 30 to 100% of yellow perch production was consumed by walleye, their principal predator. In a manipulated system, Stein et al. (1981) assessed predatory mortality of young tiger muskellunge after they were stocked in a small pond and lake. During the time of the study, a single predator (largemouth bass) accounted for 25 to 45% of losses to natural mortality.

In marine systems evidence for the relative importance of predation can be gleaned from comparing total natural mortality with estimated predatory mortality based on abundance of predators and feeding preferences. For example, multispecies cohort analyses reported by Pope and

Knights (1982) show predatory mortality as 80 to 90% of M for age-0 cod, whiting, and haddock in the North Sea (the fraction of M due to predatory mortality cannot be assessed accurately in the older ages because predators appropriate to these sizes were not included in the analysis). In another example, estimating M from energy flow models, Sissenwine (1984) demonstrated that predation in the Georges Bank ecosystem can account for all production by prey fish; nonpredatory mortality was negligible.

Thus a multitude of factors, acting alone or in concert, can be expected to produce variations in M between individuals within single groups of fish, as well as between groups. Differences can be expected between species, between stocks within species, and from place-to-place and time-to-time within given stocks. In the following section, I will review more completely existing evidence for, and the extent of, this expected variability in M.

V. VARIABILITY WITHIN AND BETWEEN GROUPS

As discussed above (Section III), simulation studies generally show that effects of choosing a particular value or set of values for M can range from insignificant to considerable, depending in part on the model used, in part on the values chosen for other parameters, and in part on the form chosen for the estimate(s) of M. Authors suggest that in the future, simulations should be conducted with a range of values for M, to bracket probable values (e.g., Beverton and Holt 1957; Tyler et al. 1985).

The problem with this advice is identifying the appropriate range and distribution of M for any given group of fish. Obviously, wide ranges for M will lead to great discrepancies between model predictions based on one end of the range or the other. It has been shown above, however, that model output can be relatively **insensitive** to small changes in M. This is particularly true if F is much larger than M (i.e., if the stock is highly exploited so that losses to fishing far exceed losses to natural mortality). The problem is determining whether, for a given stock in situ, changes in M are in fact large or small. Compensatory changes in M, in response to changes in F, will further confound the problem, because variations in M will then be a function of the value(s) of F, in addition to the suite of other factors that may be affecting estimates of M.

M does appear to vary considerably **between** groups of fish. Estimates of M compiled by Pauly (1980) (Fig. 1) for 175 stocks and species of fish worldwide differ greatly between groups, ranging from a minimum of about 0.1 year^{-1} to several unusual values as high as 7.0 year^{-1}. Even within a group as ostensibly homogeneous as the tunas, the range of estimated mortality constants spans the majority of the common values (0.2 to 2.0 year^{-1}, Murphy and Sakagawa 1977).

Estimates of variability in M **within** groups of fish are much less common, but are actually more important than the obvious differences between groups with obviously different characteristics such as differing lifespans. Most fishery analyses are directed toward understanding or predicting dynamics of single stocks (single groups of fish). The most important considerations for natural mortality parameter values in these single-species analyses are whether and if so over what values M varies for the group of fish in question.

But measuring trends or variability in natural mortality rates **within** given groups (e.g., stocks) is difficult and, with the exception of trends with age, rarely attempted. This is primarily because the only extant methods for estimating M depend either directly or indirectly on analysis of catch data (Section II), and catch data are prone to many well known (but largely unsolved) problems.

Problems with analysis of catch data fall into two general categories: 1) problems with sampling procedure, such that fish are caught or counted out of proportion to their true abundance and 2) problems with fish appearing or disappearing from the "unit stock" due to causes other than birth or natural mortality (i.e., migration, fishing mortality, or tagging mortality), again resulting in catch data that do not represent the true structure of the stock. If sampling biases can be overcome, the problem reduces to partitioning total disappearance of fish into fractions owing to fishing, tag mortality, and migration. The first partition can be eliminated by studying unfished populations, the second by quantifying tag mortality, and the third by studying only closed or tagged populations.

Unfortunately, very few sampled populations satisfy completely even one of these criteria. Regardless, we still need at least some crude estimates of M in order to determine whether M truly varies enough to invalidate the standard assumption in fisheries models that M is effectively constant during exploited ages. The question here

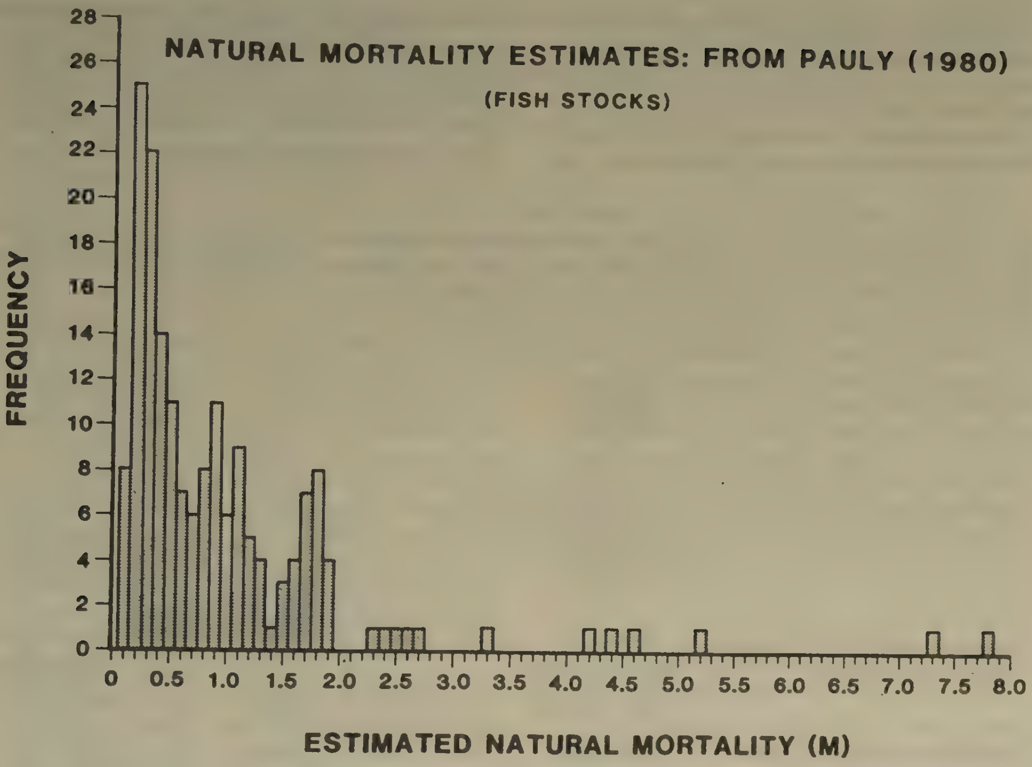

FIGURE 1.—Frequency of estimated instantaneous annual rates of natural mortality (M) in 175 different fish stocks, populations, or species. Estimates include both freshwater and marine species. Data from Pauly 1980.

concerns variability of *M* within groupings that would be used commonly to estimate *M*, such as stocks of single species, rather than general patterns across species. If *M* truly varies relatively little during these ages (so that the log of catch-at-age decreases linearly with age), if the age structure has been relatively constant historically (so that catch curves are actually linear, rather than curvilinear as seen in stocks with inconstant age structure, e.g., chapter 2, Ricker 1975), and if catch curves actually reflect relatively accurately this constancy and low variability, then most estimates of *M* derived from analysis of appropriately processed catch curves cannot help but be relatively close to the true rate. Model predictions, although in theory sensitive, would in practice be fairly robust to any particular value chosen from the true range of values for *M*.

Despite the potential problems with accuracy or precision of existing estimates from single groups of fish, I list in Table 3 most of the estimates available for unexploited populations, and some of the few existing estimates from exploited populations. My purpose is to identify the apparent range of variability in *M* within single stocks. The estimates are drawn from references cited by Pauly (1980) and other sources. Only references that reported multiple estimates for *M* are included, thus excluding most of the references reviewed. Because these estimates are derived from catch data, the stated ranges are "apparent", rather than demonstrably the "true" values.

Estimated rates of natural mortality are not particularly constant for either unexploited or exploited groups, and are only slightly less variable within stocks than they are within species. Although the range of rates within groups may appear relatively small compared to the total range of rates reported for all fish species (e.g., 0.36 to 0.56 for sauger from Lake Nipigon [Table 3] vs. approximately 0.1 to 3.0 for most species listed by Pauly 1980), the maximum and minimum rates reported for single groups differed by at least 50% in 20 of the 22 comparison listed in

Table 3. In at least one case maximum and minimum estimates differ by as much as a factor of 7 (i.e., young vs. old whitefish in Shakespeare Island Lake, Ricker 1947, Table 3).

The range of reported estimates of *M* for species (rather than single groups or stocks within a species as compared above) is even greater. Even the least variable estimates differed by a factor of 1.75 (75%, male vs. female plaice, Beverton 1964). In whitefish, the species for which the most estimates exist, maximum estimates are **20 times** greater than minimum estimates (Table 3).

TABLE 3.—Ranges in estimates of instantaneous rate of natural mortality in unexploited and exploited fish populations. M_{max}/M_{min} is expressed as the ratio between the maximum (M_{max}) and minimum (M_{min}) values reported for *M* for that species. Values in parentheses are total range of estimates and ratios for those species where multiple reports exist.

Species name	Common name	Body of water	Sex	Age (years)	*M* range	M_{max}/M_{min}	Source
I) Unexploited populations:							
Ambloplites rupestris	rock bass	Nebish Lake	m	10–12	1.47–2.1	1.49	Ricker 1947
		Nebish Lake	f	10–14	1.1–1.6	1.45	Ricker 1947
		Nebish Lake	both	10–14	1.08–1.56	1.44	Ricker 1947
					(1.08–2.1)	(2.01)	
Stizostedion canadensis	sauger	Lake Nipigon		8–14	0.36–0.56	1.56	Ricker 1947
Coregonus clupeaformis	whitefish	Lake Opeongo		6–13	0.53		Ricker 1947
		Shakespeare Island Lake		11–27	0.08–0.60	7.51	Ricker 1947
		Great Slave Lake		17–22	0.71–0.99	1.39	Kennedy 1953
		Lake Nueltin		13–15	0.84		Kennedy 1963
		Lake McDonald		11–14	1.34		Kennedy 1963
				9–10	1.66		Kennedy 1963
					(0.08–1.66)	(20.75)	
Leucichthys sardinella		Ikroavik Lake		6–10	0.2–1.4	7.00	Wohlschlag 1954
Cristovomer namayacush		Great Slave Lake		1–26	0.31–1.61	5.19	[1]Kennedy 1954
		Great Slave Lake		15–23	0.49–0.92	1.88	[1]Kennedy 1954
		Great Slave Lake		15–23	0.52–0.75	1.44	[2]Kennedy 1954
					(0.31–1.61)	(5.19)	
Perca fluviatilus	perch	River Thames	m	3–8	0.56–0.98	1.75	Williams 1967
		River Thames	f	3–7	0.2–0.64	3.20	[3]Williams 1967
		River Thames	juv	3–5	0.53–1.69	3.19	[3]Williams 1967
					(0.2–1.69)	(8.45)	
Leuciscus leuciscus	dace	River Thames		5–11	0.36–1.31	3.64	[4]Williams 1967
Alburnus alburnus	bleak	River Thames		3–8	0.6–2.4	4.00	[4]Williams 1967
Rutilus rutilus	roach	River Thames		2–11	0.22–1.38	6.27	[4]Williams 1967
		River Stour		3–12	0.44		Mann 1973
					(0.22–1.38)	(6.27)	
Cheilodactylus macropterus	tarakihi	Chatham Islands		5–35	0.03		Vooren 1977
		Chatham Islands		5–22	0.08		Vooren 1977
		New Zealand			0.15		Vooren 1977
					(0.03–0.15)	(5.00)	
II) Exploited Populations:							
Pleuronectes platessa	plaice	North Sea	f	5–13	0.08		Beverton 1964
		North Sea	m	5–13	0.14		Beverton 1964
					(0.08–0.14)	(1.75)	
Brevoortia petronus	gulf menhaden	Gulf of Mexico, Central (1969, 1971)		1–3	0.7–1.6	2.29	[5]Ahrenholz 1981
		Gulf of Mexico, Eastern (1969, 1971)		1–3	0.88–0.98	1.11	[5]Ahrenholz 1981
		Gulf of Mexico, Western (1969, 1971)		1–3	1.17–1.23	1.05	[5]Ahrenholz 1981
		Gulf of Mexico, all areas (1969, 1971)		1–3	0.95–1.2	1.26	[6]Ahrenholz 1981
					(0.7–1.6)	(2.29)	
Gadus morhua	cod	North Sea		0.5–1	0.59–1.46	2.47	[7]Pope and Knights 1982
Coregonus clupeaformis	whitefish	Lake Huron		3.8	0.34–1.67	4.91	[8]Henderson et al. 1983

[1] Increasing with age.

[2] Year to year variation (1946–52); ages 15–23 combined.

[3] Not consistent with age.

[4] Generally increasing with age.

[5] Assuming 20% tag loss rate.

[6] For tag loss rates from 10 to 30%.

[7] 8 different years (1967–75).

[8] 23 different year classes (1947–75).

As discussed previously, these different estimates can lead to at least as great a difference in results produced by fishery analyses such as yield models or stock reconstruction analyses (Section II).

Reported differences in estimates of *M* for whitefish stocks living in Shakespeare Lake compared with other relatively small lakes (e.g., Lake McDonald, Table 3) are particularly significant. Because both stocks are of the same species and living in more or less similar environments (small lakes), one might easily (and incorrectly) assume that both have the same rate of natural mortality; but they did not. The lower rates occurred in the stock occupying a small lake with no predators. This is a clear example of the effect that environment, particularly the predator environment, can have on the realized rate of natural mortality in a fish stock. Obviously, choosing a single appropriate constant for this species would be difficult. Choosing an appropriate species-specific constant for some of the other species with multiple estimates might be difficult as well (e.g., rock bass, lake trout, perch, roach, tarakihi, or menhaden, Table 3).

None of these studies from either unexploited or exploited stocks support the assumption that *M* is constant for any given stock or species, nor are these within-stock ranges particularly narrow. In addition, treatment of the original catch data may have in some cases obscured the "true" variability. Ricker (1947) and Kennedy (1953, 1954, 1963), for example, use a 3-yr smoothing technique to reduce the effects of unequal recruitment; this also serves to reduce variability that may actually be due to differences in natural mortality. Also, single estimates from data collected during only one or two years of sampling (e.g., Wohlschlag 1954; Williams 1967; Mann 1973; Vooren 1977) can be seriously biased by annual changes in either recruitment or mortality rates. If the estimates reported above are even approximately accurate, it is apparent that the range of possible values for *M* is wide, and that variability can be considerable even within single stocks.

A solution to this problem of choosing a reasonable value for *M*, at least for long-lived fish, is suggested by the possibility that variation in *M* (not just the mean value) may be related to maximum lifespan. Fish that live for many years must naturally have lower mortality rates than more short-lived fish. These lower rates may also be less variable in the longer lived stocks, if as in many other biological processes, variability is proportional to the mean. This could account for the ubiquity and apparent effectiveness of the constant 0.2 year^{-1}, used almost universally for the long-lived (20 to 30 years) and well-studied fish stocks from northern European seas (e.g., Beverton 1964). If so, assuming a constant *M* might be valid for these longer lived stocks.

Unfortunately, the few studies cited above do not support this attractive idea. Although in general, mortality rates decease as lifespan increases, the variability in estimates does not appear to follow the same trend. This may be due partially to the relatively similar lifespans (10 to 20 years) for most of the species for which estimates exist. But the apparent range in rates for the shortest lived species cited above (Ahrenholz 1981, *Brevoortia patronus*, ages 1 to 3 years, *M* range 0.7 to 1.6 year^{-1}) is certainly not greater than ranges reported for the longer lived whitefish (Henderson et al. 1983, *Coregonus clupeaformis*, ages 10+ years, *M* range 0.34 to 1.67 year^{-1}).

VI. SUMMARY AND RECOMMENDATIONS

Thus it appears that rates of *M*, or at least rates of *M* derived by existing estimation methods, do in fact vary widely within many fish stocks. Because the variations appear to be considerable and because the results from fishery models can be sensitive to large variations in *M*, one must conclude that assuming constancy without proof can have serious consequences for fishery management.

A better approach may be to discard the notion that a single "best" estimate of *M* can be found, and instead try to tailor estimates of *M* to local groups, based on some combinations of the methods discussed in Section III. Obviously, practical considerations of time and resources will limit the accuracy and precision with which *M* can be estimated. Also, the estimates in the studies reviewed here are prone to all the artifacts mentioned in the previous sections. True rates of natural mortality, and their variability, are still very poorly known for even the great stocks of commercial fish in temperature regions that have been subject to continuous exploitation for decades. Careful, repeated tagging experiments probably hold the most promise for determining with any reasonable degree of accuracy, rates of natural mortality in fish stocks. But even these have inherent problems that are not easily solved. There remains a great need both for new methods, and refinements of the old.

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Composition of the Incidental Kill of Small Cetaceans in the US Purse-Seine Fishery for Tuna in the Eastern Tropical Pacific during 1986

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ABSTRACT

Composition of incidental kill of small cetaceans by US registered purse-seiners fishing in the eastern tropical Pacific during 1986 is reported by area, species, stock, sex, length and reproductive condition. The data were collected by technicians of the Inter-American Tropical Tuna Commission and of the National Marine Fisheries Service during 47 vessel-trips.

INTRODUCTION

Several papers describing small cetacean kill incidental to fishing activities of tuna purse-seiners in the eastern tropical Pacific (ETP) have been published, as noted by Wahlen, Walker, Miller and Oliver (1986) and by Hall and Boyer (1986; 1987). In this, the fifth of a series of papers (Perrin and Oliver, 1982; Oliver, Walker and Miller, 1983; Wahlen, *et al.*, 1986; Wahlen, Miller and Macky, 1987), we report the incidental kill of small cetaceans by US registered vessels in the ETP during 1986. These kills are classified by area, species, stock, sex, length and reproductive condition. Species represented in this report are: pantropical spotted dolphins, *Stenella attenuata*; spinner dolphins, *S. longirostris*; striped dolphins, *S. coeruleoalba*; common dolphins, *Delphinus delphis*; Fraser's dolphins, *Lagenodelphis hosei*; and bottlenose dolphins, *Tursiops truncatus*.

DATA AND METHODS

Data were collected by Inter-American Tropical Tuna Commission (IATTC) and National Marine Fisheries Service (NMFS) technician-observers aboard a sample of US registered tuna purse-seine vessels fishing in the ETP (Lo, Powers and Wahlen, 1982). Data collected aboard US registered tuna seiners chartered by non-US companies were also included.

Observed kills by area, species, stock and sex, if determined, were obtained from the 'tally' databases. Length frequencies by sex and reproductive condition for females were obtained from the 'life history' databases containing extensive biological data for those dead animals which were available for 'hands-on' inspection by the technicians. The life history databases thus contain biological data for only a subset of the animals reported as killed in the tally databases, since the technicians are unable to physically examine each animal killed. See Perrin and Oliver (1982) for detailed descriptions of data recorded in these databases.

We allocated kills of offshore spotted and whitebelly spinner dolphins to geographic stocks as in Perrin and Oliver (1982). Laboratory procedures for processing specimens and determining sexual maturity are referenced in Perrin and Oliver (1982), as is the methodology of the computer programs used to summarize the reproductive condition data.

RESULTS AND DISCUSSION

Kill data were collected from each of 47 observed trips, including four trips by US seiners chartered by non-US companies. The geographical distribution of the kill is presented in Fig. 1. Kill data are summarized by stock, sex and area for 6,405 spotted dolphins (Table 1) and 2,478 spinner dolphins (Table 2); by sex and area for 792 common, 70 striped, 4 bottlenose and 68 Fraser's dolphins (Table 3); and by area only for 538 unidentified dolphins (Table 3). In Tables 1–3, which were obtained from the tally databases, the stock or species totals may be larger than the sum over sexes because the sex of some animals in the tally databases was not determined.

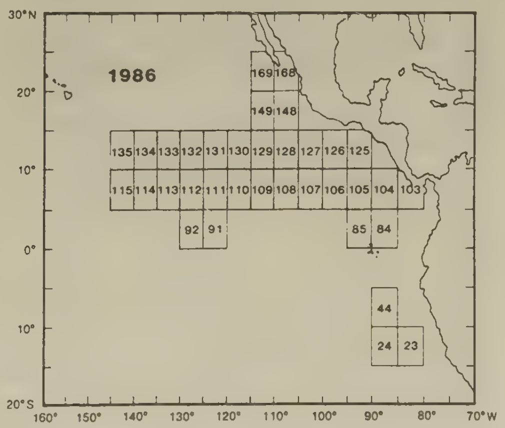

Fig. 1. Five-degree blocks in the eastern tropical Pacific Ocean in which dolphins were killed during fishing operations of US vessels in 1986. Numbered blocks without shading indicate areas in which tally data only were collected. Numbered blocks with shading indicate areas in which both tally and life history data were collected. Blocks without a number indicate areas in which no dolphin kills were recorded.

Length frequencies for sexed animals are tabulated by stock for 877 spotted and 332 spinner dolphins (Table 4) and by species for 35 common, 18 striped and 4 bottlenose dolphins (Table 5). The length frequency totals (Tables 4 and 5) are less than or equal to the kill by sex and area totals (Tables 1–3) because lengths were obtained from the life history databases, which contain data for only a subset of the animals in the tally databases. Female reproductive condition results are reported by stock for 502 spotted and 169 spinner dolphins (Table 6) and by species for 19 common and 4 striped dolphins (Table 7).

Table 1

Total kill of spotted dolphins observed by US vessels during 1986, by stock, sex (M = male, F = female), and 5° block number. No kills were reported for the coastal stock, and the reported kill of 4 unidentified spotted dolphins is not included. T = total

5° block	Northern offshore M	F	T	Southern offshore M	F	T	5° block	Northern offshore M	F	T	Southern offshore M	F	T
23	0	0	0	41	38	151	113	9	17	257	0	0	0
24	0	0	0	46	26	117	114	3	12	39	0	0	0
44	0	0	0	12	3	23	115	2	6	36	0	0	0
84	2	2	16	0	0	0	125	39	36	137	0	0	0
85	9	3	279	0	0	0	126	2	3	9	0	0	0
91	1	1	308	0	0	0	127	5	12	20	0	0	0
92	1	3	20	0	0	0	128	4	3	15	0	0	0
103	5	7	21	0	0	0	129	8	19	104	0	0	0
104	2	0	42	0	0	0	130	14	15	80	0	0	0
105	19	30	105	0	0	0	131	22	35	259	0	0	0
106	22	27	317	0	0	0	132	64	97	733	0	0	0
107	68	89	1,346	0	0	0	133	6	14	65	0	0	0
108	137	146	575	0	0	0	134	56	69	269	0	0	0
109	8	11	49	0	0	0	135	0	0	8	0	0	0
110	30	30	185	0	0	0	148	5	4	12	0	0	0
111	11	20	213	0	0	0	149	4	17	47	0	0	0
112	12	29	544	0	0	0	Total	570	757	6,110	99	67	291

Table 2

Total kill of spinner dolphins by observed US vessels during 1986, by stock, sex (M = male, F = female), and 5° block number. No kills were reported for the Costa Rican stock, and the reported kill of 42 unidentified spinner dolphins is not included

5° block	Eastern M	F	Total	Northern whitebelly M	F	Total	Southern whitebelly M	F	Total
23	0	0	0	0	0	0	0	1	2
24	0	0	0	0	0	0	5	3	11
44	0	0	0	0	0	0	0	0	2
84	0	0	3	0	0	16	0	0	0
85	0	0	0	0	0	95	0	0	0
91	0	0	0	0	0	23	0	0	0
103	23	13	44	0	0	44	0	0	0
105	0	1	2	0	0	0	0	0	0
106	0	0	1	0	0	0	0	0	0
107	4	5	26	19	21	121	0	0	0
108	3	1	10	23	24	87	0	0	0
109	2	0	23	7	1	37	0	0	0
110	11	9	49	6	3	28	0	0	0
111	0	0	1	4	8	98	0	0	0
112	3	0	3	12	10	185	0	0	0
113	0	0	0	3	4	40	0	0	0
114	0	0	0	8	3	42	0	0	0
115	0	0	0	1	5	19	0	0	0
125	13	10	47	0	0	0	0	0	0
126	4	5	12	0	0	1	0	0	0
127	8	2	33	0	0	0	0	0	0
128	20	23	72	0	0	0	0	0	0
129	11	7	49	3	1	7	0	0	0
130	8	4	34	4	2	10	0	0	0
131	15	12	192	6	3	22	0	0	0
132	17	12	160	46	46	238	0	0	0
133	0	0	0	12	10	94	0	0	0
134	0	0	0	25	32	431	0	0	0
135	0	0	0	0	0	12	0	0	0
149	0	0	10	0	0	0	0	0	0
Total	142	104	771	179	173	1,650	5	4	15

Finally, it should be noted that Hohn and Scott (1983) have identified a sampling bias in the life history data resulting from the collection process. The magnitude of the effect of this bias on the life history statistics presented here (Tables 4–7) is unknown but will probably not significantly affect life history parameter estimates (A. Hohn, Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038, USA, pers. comm. May 1986).

Table 3

Total kill of common, striped and bottlenose dolphins by observed US vessels during 1986, by sex (M = male, F = female) and 5° block number. Total kills only are included for unidentified dolphins since sex was not determined for such animals. Reported kill of 68 Fraser's dolphins (6 males, 16 females) in block number 24 is not included

5° block	Common M	F	Total	Striped M	F	Total	Bottlenose M	F	Total	Unidentified Total
85	0	0	0	0	0	0	0	0	0	30
91	0	0	0	0	0	0	0	0	0	9
103	10	13	28	0	0	0	0	0	0	0
104	80	67	555	10	14	48	0	0	0	0
105	2	6	17	0	0	0	0	0	0	0
106	10	12	31	0	0	0	0	1	1	0
107	0	0	0	9	3	13	0	0	0	50
108	0	0	0	0	0	0	0	1	1	102
109	0	0	0	0	0	0	0	0	0	248
110	0	0	0	0	0	0	0	0	0	6
111	0	0	0	0	0	0	0	0	0	2
112	0	0	0	0	0	0	0	0	0	1
125	0	0	0	0	0	0	0	1	1	0
128	0	0	0	0	0	0	0	0	0	2
129	0	0	0	0	0	0	0	0	0	4
130	0	0	0	0	0	0	0	0	0	10
131	0	0	0	0	0	1	1	0	1	63
132	0	0	0	5	1	8	0	0	0	9
133	0	0	0	0	0	0	0	0	0	2
168	0	0	6	0	0	0	0	0	0	0
169	8	15	155	0	0	0	0	0	0	0
Total	110	113	792	24	18	70	1	3	4	538

Table 4

Length frequencies of northern offshore spotted dolphins and of eastern and northern whitebelly spinner dolphins killed by observed US vessels during 1986, by sex (M = male, F = female). No kills were reported for coastal or southern offshore spotted dolphins, or for Costa Rican or southern whitebelly spinner dolphins. Reported kill of 11 unidentified spinner dolphins is not included. A = northern offshore, B = eastern, C = northern whitebelly

Length (cm)	A M	F	B M	F	C M	F	Length (cm)	A M	F	B M	F	C M	F
0– 69	0	0	0	0	0	0	150–154	5	8	2	3	4	9
70– 74	0	0	0	0	0	1	155–159	8	17	4	4	7	6
75– 79	2	0	0	0	0	0	160–164	27	21	4	6	9	15
80– 84	1	0	0	0	0	2	165–169	33	37	6	6	21	17
85– 89	0	1	0	0	0	1	170–174	41	43	4	7	22	24
90– 94	2	1	0	0	1	0	175–179	37	50	6	8	16	15
95– 99	6	1	0	0	0	1	180–184	33	65	8	3	8	13
100–104	2	2	0	0	1	0	185–189	32	77	6	1	10	5
105–109	6	4	0	0	0	0	190–194	21	76	1	0	1	0
110–114	3	3	0	0	3	0	195–199	26	37	1	0	1	1
115–119	1	4	0	1	1	0	200–204	25	16	0	0	1	0
120–124	1	4	1	2	0	0	205–209	15	4	0	0	0	0
125–129	3	4	0	1	0	2	210–214	9	2	0	0	0	0
130–134	2	3	2	0	1	0	215–219	6	0	0	0	0	0
135–139	5	4	1	2	2	2	220–224	2	0	0	0	0	0
140–144	8	8	0	1	1	4	225–	0	0	0	0	0	0
145–149	13	10	2	1	6	4	Total	375	502	48	46	116	122

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Table 5

Length frequencies of common, striped and bottlenose dolphins killed by observed US vessels during 1986, by sex (M = male, F = female). A = Common, B = striped, C = bottlenose

Length (cm)	A		B		C		Length (cm)	A		B		C	
	M	F	M	F	M	F		M	F	M	F	M	F
0–104	0	0	0	0	0	0	185–189	2	5	3	0	0	0
105–109	0	1	0	0	0	0	190–194	2	2	3	1	0	0
110–114	0	0	0	0	0	0	195–199	2	0	1	1	0	1
115–119	0	0	0	0	0	0	200–204	1	2	4	1	0	0
120–124	0	0	0	0	0	0	205–209	1	0	1	0	0	0
125–129	0	0	0	0	0	0	210–214	2	0	0	0	0	0
130–134	0	0	0	0	0	0	215–219	1	0	0	0	0	0
135–139	0	0	0	0	0	0	220–224	2	0	0	0	0	1
140–144	0	1	0	0	0	0	225–229	0	0	0	0	0	0
145–149	0	0	0	0	0	0	230–234	0	0	0	0	0	1
150–154	0	1	0	0	0	0	235–239	0	0	0	0	0	0
155–159	0	0	0	0	0	0	240–244	0	0	0	0	0	0
160–164	0	0	0	0	0	0	245–249	0	0	0	0	0	0
165–169	0	1	1	0	0	0	250–254	0	0	0	0	0	0
170–174	1	5	0	0	0	0	255–259	0	0	0	0	1	0
175–179	1	1	0	1	0	0	260–	0	0	0	0	0	0
180–184	1	0	1	0	0	0	Total	16	19	14	4	1	3

Table 6

Reproductive condition of female northern offshore spotted dolphins and of female eastern and northern whitebelly spinner dolphins killed by observed US vessels during 1986. Both sample sizes (N) and percentages (%) are indicated. Reproductive condition information was not obtained for coastal or southern offshore spotted dolphins, or for Costa Rican or southern whitebelly spinner dolphins. U = Maturity undetermined; I = Sexually immature; MU = Sexually mature, condition undetermined; P = Pregnant only; PL = Pregnant and lactating; L = Lactating only; RCL = 'Resting' with corpus luteum; R = 'Resting' without corpus luteum; PR = Post-reproductive

Reproductive condition	Northern offshore		Eastern		Northern whitebelly	
	N	%	N	%	N	%
U	235	46.8	24	52.2	64	52.0
I	107	21.3	13	28.3	35	28.5
MU	2	0.4	1	2.2	0	0.0
P	31	6.2	0	0.0	5	4.1
PL	5	1.0	0	0.0	1	0.8
L	94	18.7	6	13.0	16	13.0
RCL	5	1.0	0	0.0	1	0.8
R	23	4.6	2	4.3	1	0.8
PR	0	0.0	0	0.0	0	0.0
Total	502	100.0	46	100.0	123	100.0

Table 7

Reproductive condition of female common and striped dolphins killed by observed US vessels during 1986. Both sample sizes (N) and percentages (%) are indicated. Reproductive condition information for bottlenose dolphins is not included; none of the female bottlenose specimens was sexually mature. Abbreviations are as in Table 6

Reproductive condition	Common		Striped		Reproductive condition	Common		Striped	
	N	%	N	%		N	%	N	%
U	6	31.6	3	75.0	L	4	21.1	0	0.0
I	6	31.6	0	0.0	RCL	0	0.0	0	0.0
MU	0	0.0	0	0.0	R	0	0.0	0	0.0
P	2	10.5	1	25.0	PR	0	0.0	0	0.0
PL	1	5.3	0	0.0	Total	19	100.0	4	100.0

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GROWTH OF PACIFIC SAURY, *COLOLABIS SAIRA*, IN THE NORTHEASTERN AND NORTHWESTERN PACIFIC OCEAN[1]

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ABSTRACT

Growth of the Pacific saury, *Cololabis saira*, from the northeastern and northwestern Pacific Ocean was studied using otolith growth increments. We found that growth of Pacific sauries from the western Pacific was higher than that from the eastern Pacific. Assuming that otolith growth increments are deposited daily, average growth rates from hatching up to 1 year old were 0.62 mm/d in the eastern and 0.85 mm/d in the western Pacific. Because the growth rate changes at around 100 mm, two curves were used to model the growth of Pacific saury in the western Pacific: one for fish up to 100 mm and the other for fish larger than 100 mm. Based on counts of daily increments, Pacific sauries may be short lived. The oldest specimen examined was only 14 months old.

The Pacific saury, *Cololabis saira* (Brevoort), is distributed throughout the North Pacific Ocean and is one of the most important commercial fishes in the northwestern Pacific. The average annual catch of Pacific saury in Japan has been approximately 200,000 t (metric tons) in the last 20 years (Statistics and Information Department, Japan 1985). The catch has varied by an order of magnitude in the last 20 years from a minimum of 63,000 t in 1969 to a maximum of 406,000 t in 1973. Fluctuation in stock size is a major factor in catch variability although economic factors such as fish price may also affect total landings. However, the causes of stock fluctuation in the western Pacific remain unknown. In the eastern Pacific, the Pacific saury has not been exploited but is recognized as a potential fishery resource (Ahlstrom 1968; Smith et al. 1970).

Investigations of the Pacific saury have mainly been devoted to such subjects as systematics, abundance, distribution, migration, and formation of fishing ground in relation to oceanographic conditions (e.g., Hubbs and Wisner 1980; Smith et al. 1970; Odate 1977; Fukushima 1979; Sablin and Pavlychev 1982; Gong 1984). Age determination and growth, however, remain controversial (Hatanaka 1955; Hotta 1960; Novikov 1960; Sunada 1974; Kim and Park 1981), notwithstanding their critical importance for fish stock assessment.

The discovery of daily increments in the otoliths of fishes (Pannella 1971) has made it possible to estimate age and growth of larval and juvenile fishes accurately. Daily increments have been used to age many species of fishes (Jones 1986). Nishimura et al. (1985) reported the presence of growth increments in Pacific saury otoliths observed by scanning electron microscopy and suggested that it is possible to estimate age and growth of Pacific saury by using daily increments in the otolith. The purpose of this paper is to determine the age of Pacific sauries from the eastern and western North Pacific using daily increments and to compare the growth rates in these areas.

MATERIALS AND METHODS

We read otoliths of 75 Pacific sauries from the northeastern and 172 from the northwestern Pacific Ocean. Details of sampling and methods of reading otoliths are summarized in Table 1 and Figure 1. Additional samples from the western Pacific were used to determine the relation between otolith size and fish length. Fish from the eastern Pacific were fixed and preserved in 80% alcohol after capture, and those from the western Pacific were stored frozen and thawed when processed. Because specimens frequently have damaged upper jaws, knob length (the distance from the tip of the lower jaw to the posterior end of the muscular knob at the base of a caudal peduncle) is the standard measure of body size in Pacific saury. All body lengths in this paper are knob length.

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TABLE 1.—Collection records of saury samples from the eastern (# 1–10) and the western (# 11–22) North Pacific. N = Neuston net; G = Gill net; D = Dip net.

		Location					
Sample	Date	Lat.	Long.	No.	Size range (KnL mm)	Gear	Micro-scope
1	80 06 29	36°02′N	124°04′W	10	19.8–109.0	N	LM
2	80 06 29	36°07′N	123°55′W	10	19.8– 66.0	N	LM
3	80 06 29	36°07′N	123°45′W	10	15.3– 96.0	N	LM
4	81 10 26	46°36′N	127°49′W	5	47.8–235.0	N	LM
5	81 10 27	47°19′N	126°09′W	6	38.0–142.0	N	LM
6	81 10 28	47°20′N	124°30′W	12	23.9–216.0	N	LM
7	81 10 29	46°21′N	127°38′W	1	209.0	N	LM
8	81 10 30	46°38′N	125°54′W	14	20.6– 85.0	N	LM
9	81 11 01	45°21′N	127°38′W	4	27.0– 71.0	N	LM
10	81 11 02	45°38′N	124°51′W	3	70.0–206.0	N	LM
11	84 05 26	37°01′N	164°02′E	19	145.0–230.0	G	SEM
12	84 06 02	37°00′N	158°00′E	114	38.0–125.0	N	SEM
13	84 07 16	42°00′N	172°00′E	7	213.0–282.0	G	SEM
14	84 10 06	43°09′N	153°14′E	5	300.0–330.0	D	SEM
15	85 05 20	36°00′N	150°00′E	3	21.0– 69.5	N	LM
16	85 05 21	38°15′N	149°59′E	2	8.3– 12.5	N	LM
17	85 05 23	38°30′N	152°00′E	2	26.5– 45.5	N	LM
18	85 05 24	38°00′N	152°00′E	9	29.0– 85.0	N	LM
19	85 05 29	38°45′N	156°00′E	3	16.0– 33.5	N	LM
20	85 05 29	38°30′N	156°00′E	2	27.0– 33.0	N	LM
21	85 05 29	38°15′N	156°00′E	3	24.6– 65.0	N	LM
22	85 05 30	38°00′N	156°00′E	3	31.5– 68.5	N	LM

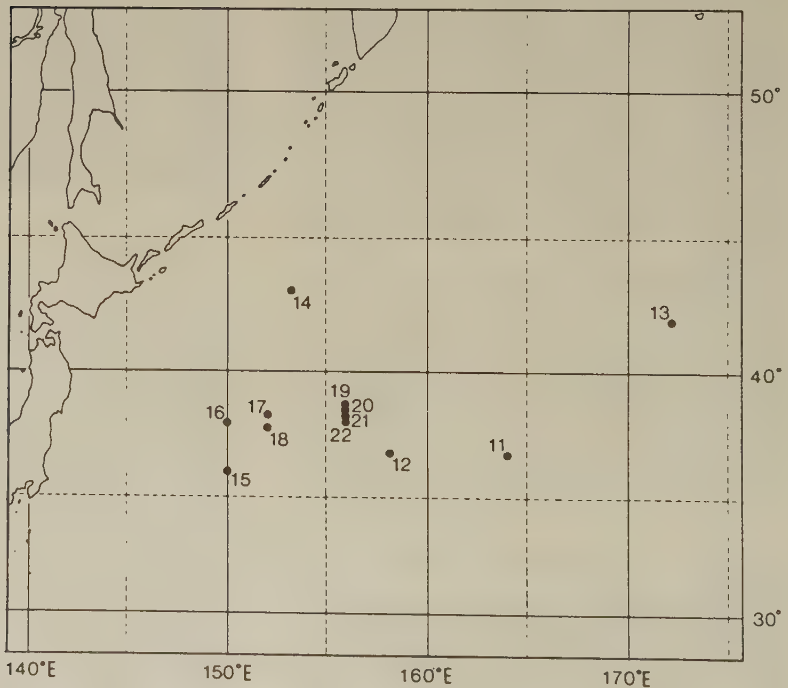
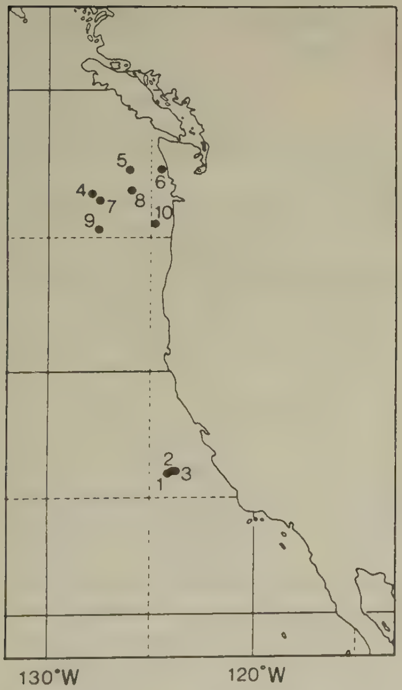


FIGURE 1.—Locations of Pacific saury collection in the North Pacific. Figures by

Sagittae were dissected out from fish and left to dry after removing tissues and membranes. We used a dissecting microscope with a polarizing filter to dissect otoliths from small larvae and juveniles. The otoliths were read either by light microscopy (LM) or by scanning electron microscopy (SEM). Otoliths that were to be read by LM were mounted in EUKITT[5] after dissection. Otolith radius was measured from the focus to posterior margin and the increments were counted along the same transect using the otolith reading system, which was developed by the Southwest Fisheries Center of the National Marine Fisheries Service, NOAA, and which consists of a light microscope, a video monitor, a micro-computer, and a digitizer (Methot 1981).

For SEM, otoliths were mounted in epoxy or methacrylate resin. The otolith radius was measured from the focus to the posterior margin with an optical comparator. The otoliths were ground oblique to the sagittal plane parallel to the long axis of the otolith in order to have a flat plane through the otolith nucleus. The polished surface was washed in xylene, using an ultrasonic washer, then dried and etched for 50 seconds with 0.2M EDTA-2Na (disodium ethylenediaminetetraacetic acid). The etched surface was coated with palladium platinum and observed under an SEM (JSM-25) at 15 kV.



dots indicate sample numbers in Table 1.

The three authors of this paper read saury otoliths independently: the senior author read fish from the western Pacific up to 85 mm by LM, the second author read otoliths from the eastern Pacific by LM, and the third read otoliths from the western Pacific larger than 38 mm by SEM. To confirm that we were all interpreting the same structure as growth rings by SEM and LM, we compared 50 data points read by SEM and 14 points read by LM for western Pacific sauries between 38 and 85 mm. The distribution of increment number versus knob length was the same. We also checked for possible biases for the two readers using LM by having each read the same set of otoliths independently.

RESULTS

The nucleus of a Pacific saury sagitta is approximately 20 μm in diameter and is composed of four to six small dense bodies which appear to be assemblages of calcareous spherules (Fig. 2a). These dense bodies are separated from one another and each is surrounded by a small concentric ring.

We observed the nucleus areas of otoliths from Pacific sauries collected in the western Pacific in 1985 (sample # 15–22) and found that most of them had a distinct ring of about 27 μm in radius. Between the nucleus and this distinct ring, four (or five) indistinct growth rings were detected (Fig. 2b).

We measured knob lengths of 27 larval and juvenile Pacific sauries before freezing and after thawing, and found that the ratio of these two measurements was 0.997. There was virtually no shrinkage by freezing and thawing. Theilacker (1980) found that preservation of larval northern anchovy, *Engraulis mordax*, in 80% alcohol did not cause additional shrinkage of the body after net treatment. Thus, knob lengths after both 80% alcohol preservation and freezing are comparable to each other, and this measurement corresponds to the size after net treatment. Since shrinkage factors by net treatment are not known for the saury, lengths are uncorrected for net shrinkage.

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[5] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

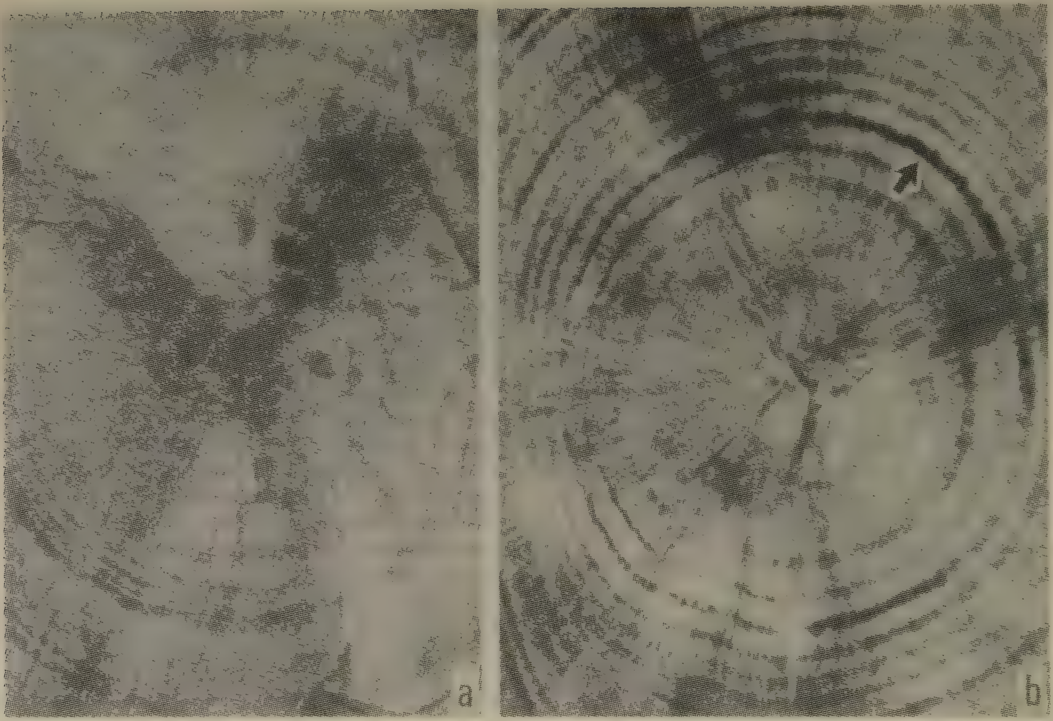

FIGURE 2.—Light micrographs of Pacific saury sagittae. a) Otolith nucleus composed of 5 or 6 separate dense bodies with surrounding cores. b) Assumed 4 embryonic and 1 hatching (arrow) rings.

The daily periodicity of growth increment formation in the Pacific saury has not been verified. For that reason we plotted the number of increments versus knob length instead of age versus length. We used the Laird-Gompertz equation to describe the relations of increment number and length as growth curves for both the eastern and western Pacific saury. Hatching size of artificially fertilized and incubated Pacific saury from the western Pacific was reported to be 7.19 mm in average live total length (Yusa 1960). From the drawing of a newly hatched larva in Yusa's paper, we estimated live knob length to be 6.60 mm. Shrinkage factors of northern anchovy in the size range from 6.00 to 7.99 mm were 0.90 for a 5-min net treatment and 0.85 for a 10-min net treatment (Theilacker 1980). Using these values, the capture size of a newly hatched larva of Pacific saury after a 5-min net treatment was estimated to be 5.95 mm and a 10-min treatment to be 5.61 mm. We fixed the hatching size from 5.85 to 5.95 mm in the growth curve, because the Pacific saury larvae at this size are in a more advanced developmental stage and shrank less by net treatment than northern anchovy.

The resulting growth equation for the eastern Pacific saury was

$$KnL = 5.85 \exp((0.0427/0.115)(1 - e^{(-0.0115(I-5))}))$$

and the equation for the western Pacific saury was

$$KnL = 5.95 \exp((0.0504/0.0128)(1 - e^{(-0.0128(I-5))}))$$

where *KnL* is a knob length in mm and *I* is the total number of increments observed in an otolith. The term, $I-5$, indicates that five increments were presumed to have been present at hatching. Data from the western Pacific saury appear to consist of two curves separated around 100 mm in *KnL*. Two Laird-Gompertz curves fit much better than one curve. The intersection of the two curves was at 114 increments and 100 mm. The growth equation for fish smaller than 100 mm was

$$KnL = 5.90 \exp((0.0865/0.0293)(1 - e^{(-0.0293(I-5))}))$$

and for fish larger than 100 mm *KnL* was

$$KnL = 3.01 \exp((0.0592/0.0126)(1 - e^{(-0.0126(I-5))}))$$

The estimated mean square error, 215.7, of the two curves was smaller than that for a single curve, 351.7. The two-curve model fits much better for the smaller size range up to 100 mm. The estimated mean square error of the two-curve model for this size range, 75.7, was much smaller than that of the one-curve model, 240.8.

The growth rate of Pacific saury in the eastern Pacific was slower than that in the western Pacific (Figs. 3, 4). The knob length of saury in the eastern Pacific would be about 75 mm at 100 rings, 170 mm at 200 rings, and 220 mm at 300 rings, whereas in the western Pacific knob length would be about 100 mm at 100 rings, 230 mm at 200 rings, and 300 mm at 300 rings. Assuming that the rings are formed daily, overall growth rates of the first one year of their life were 0.62 mm/d and 0.85 mm/d for the eastern and western Pacific Ocean, respectively.

The largest specimen examined was 330 mm from the western Pacific, which had 328 increments, and the oldest fish, also from the western Pacific, which measured 320 mm, had only 418 increments. These fish would be classified as very large or large by Novikov's categories of fish size composition (Novikov 1960, 1973). The largest fish examined from the eastern Pacific was 235 mm and had 241 increments. Hughes (1974), however, reported larger fish from the eastern Pacific.

In Pacific saury from the western Pacific, the relation between otolith radius in μm (OR) and knob length in mm (*KnL*) was linear on logarithm-logarithm coordinates (Fig. 5). The equation computed by the geometric mean regression (Ricker 1973) was

$$\ln(\mathrm{OR}) = 2.33 + 0.749 \ln(KnL) \quad (r = 0.979).$$

The otolith radius at hatching (5.9 mm *KnL*) calculated by this formula was 38.9 μm, which was 12 μm larger than the radius of the presumed hatching ring.

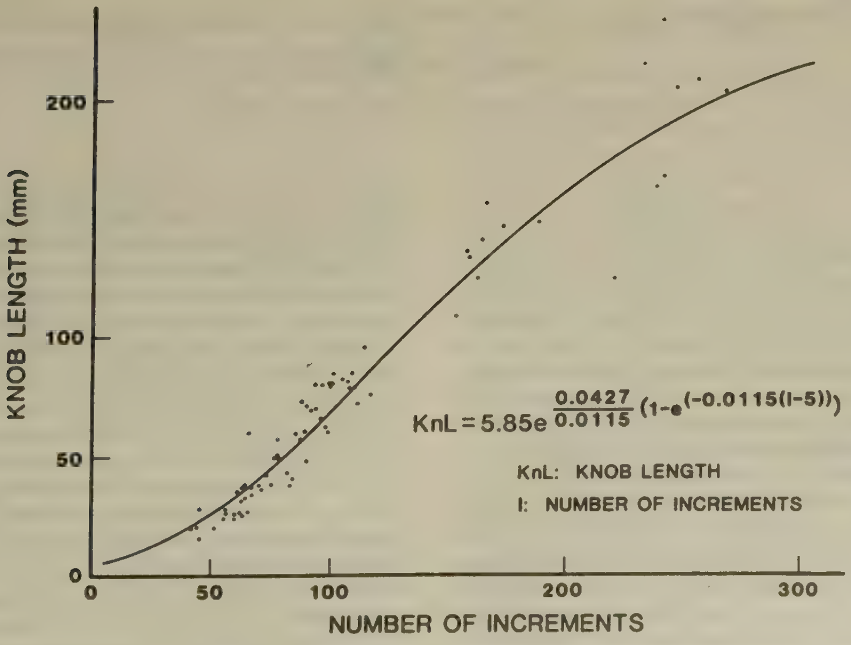

FIGURE 3.—Growth curve of the eastern Pacific saury.

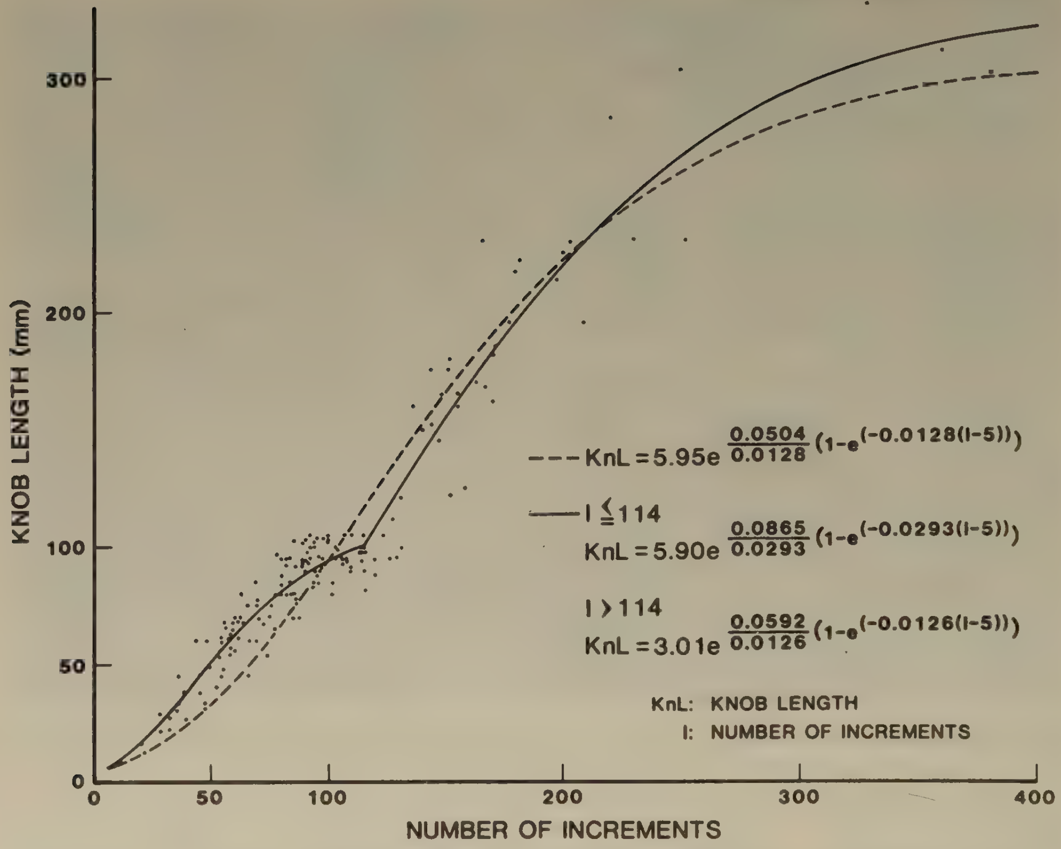

FIGURE 4.—Growth curve of the western Pacific saury.

DISCUSSION

The microstructure of otolith growth increments of the Pacific saury is similar to that of daily increments in some other fishes (Nishimura et al. 1985). Thus, the following discussion is based on the assumption that the increments are daily growth rings. A rearing experiment of larval sauries is under way in the senior author's laboratory to verify daily periodicity of the increment formation.

Formation of a few embryonic growth rings or a lamellar structure has been reported in California grunion, *Leuresthes tenuis*, (Brothers et al. 1976); mummichog, *Fundulus heteroclitus*, (Radtke and Dean 1982); and walleye pollock, *Theragra chalcogramma*, (Nishimura and Yamada 1984). Radtke and Dean (1982) mentioned that deposition of growth rings in the embryonic stage might be related to a long incubation period. Pacific saury has a long incubation period—about 17 days under 13.5°–15.7°C (Yusa 1960). At this temperature, eye pigmentation begins 7 or 8 days before hatching, and pectoral fins show constant movement from 5 or 6 days before hatching (Yusa 1960). Notochord flexion occurs about midway through embryonic development at 14°–22°C (Uchida et al. 1958). Thus saury is more advanced at hatching than killifish based on the embryonic development of killifish reported by Armstrong and Child (1965). Observing the central area of otoliths, we found four faint rings and a dark ring immediately outside of those rings. We assumed therefore that the four faint rings are embryonic rings and the dark ring is the hatching ring. This assumption may be confirmed by examining otoliths of late embryos and newly hatched larvae of saury.

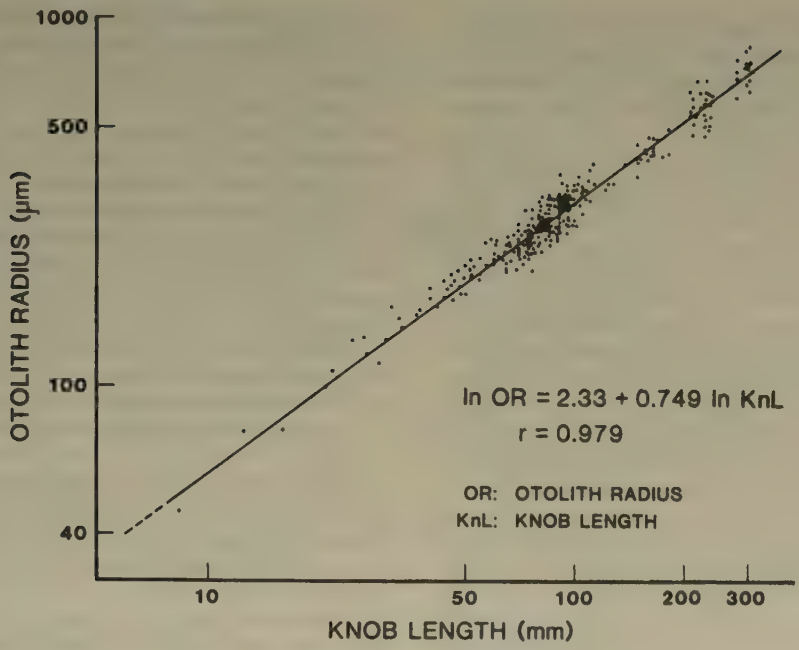

FIGURE 5.—Knob length and otolith radius relationship of the western Pacific saury.

Previous studies on age and growth of the Pacific saury have based on annuli on scales and/or otoliths. Sunada (1974) found five age groups in Pacific sauries off southern Oregon, California, and Baja California. Mean fork lengths of age groups were 171, 220, 246, 270, and 268 mm for age 0, 1, 2, 3, and 4, respectively. Hughes (1974) examined age composition of 5,248 sauries collected in waters off California up to Vancouver Island. He found spring- and autumn-born fish in his samples, but little difference was noted in growth rates between two groups. Approximate knob lengths of 1.0- to 5.0-year-old fish were 180, 230, 255, 290, 310 mm. The growth rates given in these two papers are not very much different. The saury grows at 0.5–0.6 mm/d up to 1 year old, which is almost equal to our growth rate in the eastern Pacific, 0.62 mm/d. Hatanaka (1955) found five age groups in the western population of the saury, 0–4 years old, and estimated mean body length of age groups to be 80, 160, 230, 265 mm for 1- to 4-year-old fish, respectively. Novikov (1960, 1973) divided sauries captured in autumn into five size groups, very small (–200 mm), small (201–240), medium (241–290), large (291–320), and very large (321+), and assigned the small, medium, and large to 1-, 2-, and 3-year-old with maximum 5-year-old fish.

A different model of Pacific saury growth in the western Pacific was proposed by Hotta (1960) based upon a hypothesis of two subpopulations. He separated the saury into spring-spawning and autumn-spawning populations based upon the observations of fish size composition, scales, otoliths, and numbers of vertebrae. He assigned four ages of half year intervals, 1.0, 1.5, 2.0, 2.5 years old, to fish 210–240, 260–280, 290–300, and 310–330 mm, respectively. The growth rate up to 1 year was 0.6–0.7 mm/d. Kim and Park (1981) examined Pacific sauries from Korean waters and found four size groups of four different ages of half-year intervals as well. They presented two growth models for each of two subpopulations, spring and autumn spawning, based upon the von Bertalanffy equation. The sizes at ages were almost identical to those of Hotta (1960). However, the hypothesis of two saury subpopulations in the western Pacific is not supported by electrophoretic analyses of genetic separation (Numachi 1971; Hara et al. 1982).

The average growth rate of the western Pacific saury in this paper was 1.1 mm/d from 0 to 8 or

9 months old. It was still faster than Novikov's growth rate of the corresponding age period (0.83 mm/d), which was the highest rate of all the previous reports. The fish would become 316 mm in one year according to our model.

Support for the fast growth rate of Pacific saury presented in this paper in the western Pacific can be found in rearing experiments. Hotta (1958) reared young sauries caught by a set net. He reared them in a crawl and fed them minced anchovy and mackerel twice a day. Young sauries 116 mm in mean length became 172 mm in the rearing period after 72 days. The growth rate was 0.78 mm/d. The sauries fed three times a day grew 130–143% faster than the group fed twice a day. Thus growth rates of young sauries may be higher than 1.1 mm/d (0.78 × 1.4 mm/d) when food is readily available. Our growth rate of sauries in this size range was approximately 1.5 mm/d in the western Pacific. For Atlantic saury, *Scomberesox saurus scombroides*, reared by Brownell (1983), the average growth rate of the larvae was 0.62 mm/d from hatching (7.5 mm SL) to 47-day old (36.8 mm SL). The growth rates of *Cololabis saira* in a corresponding period were 0.48 mm/d in the eastern Pacific and 1.0 mm/d in the western Pacific.

Our results indicate that the growth rate of Pacific saury in the western Pacific is much higher than in the eastern Pacific. This could be due to a difference in food availability between the two areas. However, mean zooplankton standing stock in 1951–66 was 34.8 g/m^2 in the California Current region in June (Smith and Eppley 1982), whereas that of Kuroshio water off southern Japan was 4.7 g/m^2 and of Oyashio area off northern Japan was 25.7 g/m^2 in May to July (Odate 1986). Thus, differences in zooplankton standing stock do not explain the difference in growth rates.

On the other hand, there seems to be a reasonable explanation for the reacceleration of growth rate at around 100 mm in the western Pacific saury. The western sauries hatch out mainly in offshore water of the Kuroshio Current (lat. 31–33°N) off Japan in winter. They migrate north to the Oyashio area (up to 46–50°N) where copepods are highly available. Young and adult sauries feed actively and gain fat. They are in the northward migration stage in early summer when they are about 100 mm, and are moving from poor Kuroshio water to rich Oyashio water (Fukushima 1979). High zooplankton standing stock in the Oyashio water and its derivatives might be responsible for the reacceleration of growth rate in fish older than 100 days.

The growth rates of Pacific saury in the western Pacific may differ from year-to-year due to environmental factors and may result in changes in size composition of the fish. Between 1968 and 1972, mean knob length of exploited sauries in the western Pacific was 170-250 mm, whereas in the 1980's the major mode in the size composition was 290-310 mm (S. Kosaka[6]). This increase could have been due to an acceleration of growth rate or a shift of spawning season to early months or both in recent years. The high growth rate of western Pacific saury presented in this paper has come from specimens collected in 1984 and 1985. The growth rate in the late 1960's and early 1970's may have been lower than that presented in this paper. Investigation of the interannual variation in growth rates using daily increments would distinguish between these two hypotheses.

We used three different gears to collect Pacific saury samples in the western Pacific. Knob lengths of sauries collected were from 8.3 to 125 mm by ring net, 145 to 282 mm by gill net, and 300 to 330 mm by stick-held dip net. Sauries of 125–145 mm might not be available either to the ring net or to the gill net. Further, the ring net may select small juveniles of a cohort in the size range over 100 mm, and this may have produced the two growth curves. This problem needs to be examined further with data on gear selectivity.

We do not know how long Pacific sauries survive after becoming adult. The oldest specimen in our sample was about 14 months old after hatching (418 increments). The largest saury aged (330 mm), which had 328 growth rings, is close to the maximum size. Although the maximum known length of the Pacific saury was reported to be about 400 mm (Hubbs and Wisner 1980), the largest fish exploited in Japan is about 340 mm. Therefore, the lifespan of the Pacific saury is about one year in the western Pacific. Our results are more consistent with those of Kosaka (1979) who found two age groups (0 and 1 year) than those (Sablin 1979) who found three age groups (0, 1, and 2 years).

In Japan, fishing efforts of the Pacific saury is regulated by fishing season as well as by the number of fishing boats. The fishing season starts in mid-August. Pacific sauries hatched in the main spawning season are about 250 days old at this time of year (approximately 270 mm) and are growing at the rate of 0.8 mm/d. Thus a 2-wk postponement at the beginning of fishing season would result in an 11 mm (10–15 g body weight) increase of average fish length. The biomass and yield of Pacific saury need to be reestimated based on faster growth rates presented here.

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A COMPREHENSIVE THEORY ON THE ETIOLOGY OF BURNT TUNA

CHERYL WATSON,[1] ROBERT E. BOURKE,[2] AND RICHARD W. BRILL[3]

ABSTRACT

Over the past 14 years, the Hawaii handline fishery has experienced phenomenal growth in the catch for large yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *Thunnus obesus*. These fish are primarily caught for the sashimi (raw consumption) market but have been continually plagued with a product quality problem known as "burnt tuna" or, in Japanese, yake niku. Not only does this problem significantly reduce the value of the catch, it also limits export markets and expansion of this low-capital, high-return fishery to other areas of the Pacific. Previous research and suggestions for mitigating burnt tuna have centered on the hypothesis that it is caused by high muscle temperature and low pH, which is the result of a violent struggle during capture.

A new, more comprehensive hypothesis is presented: Burnt tuna is actually caused by the post-mortem activation of enzymes known as calcium-activated proteases and by the enhancement of the effect of these enzymes by high blood catecholamine levels. Previously unexplainable observations, such as the propensity of female fish to become burnt more often during the summer months, the efficacy of brain destruction in preventing burnt tuna, and the lack of effect of cooling on the incidence of burnt tuna, are explainable in light of this new hypothesis.

One of the largest fisheries in Hawaii is the handline fishery for large (>50 kg) yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *T. obesus*, caught primarily for raw consumption as sashimi. Yearly landings increased from 89 short tons (ex-vessel value, $131,000) in 1973 to 615 short tons (ex-vessel value, $2.1 million) in 1984 (Yuen 1979; Hudgins and Pooley 1987). The total economic value of the fishery has been estimated as high as $5 million yearly (Ikehara[4]). In Hawaii, the night handline fishery is known as ika shibi from the Japanese words for squid and tuna, and the daytime fishery is known as palu ahi from the Hawaiian words for chum and yellowfin tuna. There is also growing international interest in this type of fishing because of its low initial capital investment, low operating and fixed expenses, strong export markets, and high profitability (Strong 1979; Gibson 1981; Jerrett 1984). Boats can be as small as 6 m and require only one- or two-man crew. Catch rates in Hawaii have ranged from two fish per hook per night (Yuen 1979) to one-half fish per hook per night (Bourke[5]), illustrating the profitability for the individual fisherman.

Unfortunately, handline (as well as primarily recreational trolling) fishermen are plagued by a product quality problem known as "burnt tuna" or, in Japanese, as yake niku (literally translated as "cooked meat"). When fish are intended for raw consumption, product quality is of utmost importance. Prime quality tuna flesh should be red, translucent, and firm and have a delicate flavor. Burnt tuna is pale, exudes a clear fluid, and has a soft texture and a slightly sour taste. Although perfectly palatable when cooked or canned, burnt tuna is considered unsuitable for raw consumption and commands only a fraction of the price of prime quality fish. Fish are usually exported whole to preserve freshness, so burnt tuna often is not detected until shipping costs have been incurred. This discourages exports of tuna caught from areas or via fishing techniques with high incidences of the problem.

Burnt tuna affects from 5 to 100% of the tissue from an individual fish and ranges from mild to severe. Approximately 25% of the fish caught by the Hawaii handline fishery are burnt, as are 50% of the large yellowfin tuna caught by commercial and recreational trollers (Bourke fn. 5).

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Annual losses to the handline fishery are an estimated 16% of the value of the total catch (Cramer et al. 1981). The problem has also been reported in fish intended for raw consumption caught by purse seine (Nakamura et al. 1977). Surprisingly, the problem rarely occurs in fish caught by longlining (Williams 1986).

PAST RESEARCH ON BURNT TUNA

The Japanese were the first to investigate the causes of burnt tuna and possible mitigating strategies (Itokawa 1968, 1969). The first controlled laboratory investigations were those of Nakamura et al. (1977) and Konagaya and Konagaya (1978, 1979). Nakamura et al. (1977) concluded that high muscle temperature and low muscle pH caused myofibrillar protein denaturation and also noticed that, once denaturation began, it continued even if the tissue was kept at 0°C. Because of the relatively high thermostability of tuna myofibrillar protein and because yake niku occurs in species (e.g., frigate mackerel and sardine) that do not generate high muscle temperatures during struggling, Konagaya and Konagaya (1978) concluded that acid denaturation of myofibrillar proteins at moderate temperatures was the underlying cause.

Cramer et al. (1981) studied handline-caught yellowfin tuna in Hawaii and found that the occurrence of burnt tuna did not correlate with muscle temperature at time of landing and correlated only loosely with extracellular muscle pH. Ikehara[6] conducted an engineering study to develop methods to cool large yellowfin tuna more rapidly, the presumption being that rapid cooling would prevent muscle degradation. Although successful in developing a technique to increase cooling of deep muscle temperature, as shown in Figure 1, there was no apparent correlation between rate of cooling and incidence of burnt flesh. In spite of this lack of directly observed correlation, some publications designed for fishermen still stress that high muscle temperatures and low muscle pH are the prime causes of burnt tuna (Gibson 1981). Others have expressed doubt as to the validity of this hypothesis (Jerrett 1984).

The high muscle temperature-low pH hypothesis appears to fit with what is known about tuna physiology, in that these fishes are capable of producing muscle temperatures significantly above ambient (Carey et al. 1971; Carey 1973) and exhibit some of the highest rates of muscle glycolysis (production of muscle lactate and concomitant production of acidity) observed in nature (Hochachka et al. 1978; Hochachka and Mommsen 1983). Yet some observations do not fit this hypothesis. For example, burnt tuna occurs more frequently in summer, more frequently in female fish, and more frequently in fish fought for short periods of time than in fish fought for long periods (>7 minutes or <2 hours) (Davie and Sparksman 1986; Nakamura[7]). Furthermore, burnt tuna occurs rarely in longline-caught fish and in fish subjected to brain or spinal column destruction immediately following capture (Nakamura et al. 1977; [Suisan Sekai] 1977; Cramer et al. 1981; Davie and Sparksman 1986; Nakamura fn. 7). The hypothesis that burnt tuna is caused by high muscle temperature and low muscle pH does not seem to directly fit with any of these observations.

A NEW ANALYSIS OF THE BURNT TUNA PROBLEM

At the biochemical level, the high muscle temperature-low pH hypothesis would predict that the observed drop in extracellular pH would be accompanied by a similar drop in intracellular pH and activation of lysosomal proteases. These proteases would then degrade actin and myosin, the dominant muscular proteins, resulting in the

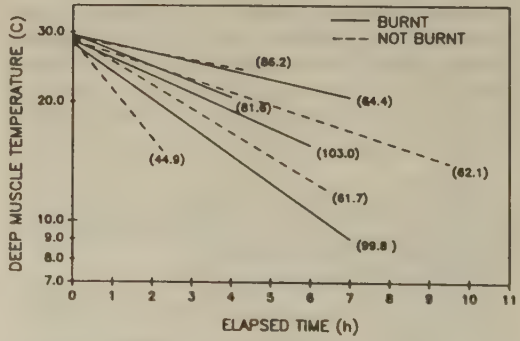

FIGURE 1.—Data are from Ikehara (text fn. 6). Initial and final deep muscle temperatures are plotted on semilogarithmic axes to linearize the rate of temperature change. Numbers in parentheses are the body weight (kg) for each fish.

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[6] Ikehara, W. N. 1981. Development of a small-boat chilling system for the reduction of burnt tuna. Final Report for a Pacific Tuna Development Foundation contract, var. pag.

[7] R. Nakamura, Department of Animal Sciences, University of Hawaii, Honolulu, HI 96822, pers. commun. October 1987.

undesirable changes seen in burnt tuna. The lysosomal proteases, specifically cathepsins B, D, and L, have an optimum pH of about 5 (Dahlmann et al. 1984). However, recent work by Abe et al. (1985, 1986) has shown that, intracellularly, tuna muscle is well buffered and that a fall in extracellular pH is not necessarily accompanied by an equivalent fall in intracellular pH. Using ischemic rat gastrocnemius muscle, Hagberg (1985) found that a 1 pH unit drop (7.30–6.36) in extracellular pH was accompanied by a drop in intracellular pH of only 0.4 unit (7.00–6.60). Thus, the acidic intracellular environment that would favor the action of the lysosomal proteases probably is not present in burnt tuna. Also, with the exception of calcium-activated neutral protease, all other muscle proteases (cathepsins B, D, L; alkaline serine protease; neutral trypsin-like protease; and alkaline cysteinyl protease) degrade myosin (Dahlmann et al. 1984). Yet Hochachka and Brill (1987) found burnt muscle had no increase in 3-methyl-histidine, a specific marker for myosin breakdown. Decomposition of other myofibrillar proteins is, therefore, implicated.

Electronmicrographs of postmortem burnt tuna muscle (Davie and Sparksman 1986) showed a consistent, rapid disintegration of Z-discs and irregularities in the sarcoplasmic reticulum (SR). The changes in burnt muscle were not different in kind from postmortem changes seen in unburnt tissue, but were a result of a significant increase in the rate of disintegration. Selected destruction of the Z-discs, troponin and tropomyosin, and the SR is characteristic of a pair of proteases known as calcium-activated neutral proteases (CANP's) (Sugita et al. 1984; Suzuki et al. 1984). These proteases are cytoplasmic, ubiquitous, activated by increased intracellular calcium levels, and active at pH 5.5–8.0 (Sakamoto and Seki 1985; Koohmaraie et al. 1986; Seki and Kimura 1986; Zeece et al. 1986b). The intracellular pH most likely found in burnt tuna muscle is, therefore, more consistent with CANP action than with lysosomal proteases whose activity requires a pH closer to 4.5 (Hochachka and Brill 1987). In addition, while cathepsin D's activity is greatly restricted at 15°C, CANP is still active at 5°C (Koohmaraie et al. 1986; Zeece et al. 1986a).

A new etiology of burnt tuna proposed by Hochachka and Brill (1987) is summarized in Figure 2. Their hypothesis predicts that low intracellular ATP concentrations lead to the leaking of Ca^{++} into the cell and increases in intracellular Ca^{++} concentrations. These increases, in turn, activate CANP, which specifically attacks troponin, tropomyosin, SR, and mitochondria. The breakdown of the latter two intracellular organelles releases more calcium into the cytoplasm, thus further increasing the activity of CANP.

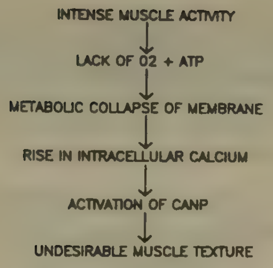
INTENSE MUSCLE ACTIVITY
LACK OF O2 + ATP
METABOLIC COLLAPSE OF MEMBRANE
RISE IN INTRACELLULAR CALCIUM
ACTIVATION OF CANP
UNDESIRABLE MUSCLE TEXTURE

FIGURE 2.—Biochemical reactions involved in the development of burnt tuna as proposed by Hochachka and Brill (1987).

The effect of brain and spinal cord destruction on reducing the incidence of burnt tuna and of similar muscle degradation seen in other fish species can be explained by this new hypothesis, which assumes the initial drop in ATP is the root cause of the elevated intracellular calcium (Amano et al. 1953; Fujimaki and Kojo 1953; Konagaya and Konagaya 1978; Ikehara fn. 6). Brain destruction maintains elevated muscle ATP levels after capture (Boyd et al. 1984). Data recently collected on the use of brain and spinal cord destruction in large yellowfin tuna (Fig. 3)

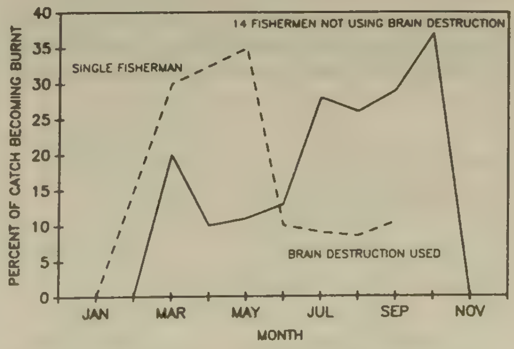

FIGURE 3.—Incidence of burnt tuna occurring in large yellowfin tuna caught by 14 commercial handline fishermen operating out of Hilo, HI, January–September 1984, and by 1 fisherman who began using brain destruction in May. His incidence of fish becoming burnt dropped dramatically in spite of the normal summer increased incidence seen in the catch of 14 other fishermen.

clearly show the effectiveness of this technique in preventing burnt tuna. A drop from 30 to <10% of the tuna becoming burnt was noted when the fisherman changed his killing technique from shooting to the use of a brain spike.

A MORE COMPREHENSIVE HYPOTHESIS ON THE ETIOLOGY OF BURNT TUNA

The hypothesis presented by Hochachka and Brill (1987) does not explain all the observed factors leading to tunas' different propensity to become burnt. It cannot explain why tunas struggling for <7 minutes rarely become burnt (Nakamura fn. 7), nor can it account for the observations of Davie and Sparksman (1986) and Bourke (unpubl. data), who found that tuna struggling for extended (>1 hour) periods of time have a lower probability of becoming burnt. It also cannot explain why female fish become burnt more often than males (Nakamura et al. 1977), or why fish caught in summer become burnt more often (Fig. 3).

Our revised hypothesis is presented in Figure 4. We have incorporated into the Hochachka and Brill (1987) hypothesis, the action of the neurotransmitters-hormones norepinephrine (NE) and epinephrine (E) (collectively referred to as catecholamines). Periods of intense physical activity or capture stress increase the levels of circulating catecholamines by about 10–200 times in fish other than tunas (Nakano and Tomlinson 1967; Ling and Wells 1985). Most likely a similar situation occurs in tuna during hooking, fighting, and capture. The importance of elevated circulating catecholamines in this particular schema comes from their potentiating effect on the action of CANP. Catecholamines cause the phosphorylation of troponin, resulting in a more rapid and prolonged proteolysis of this muscle structure (Toyo-oka 1982); in other words, high circulating levels of catecholamines greatly increase the effectiveness of the enzymes responsible for a tuna becoming burnt.[8]

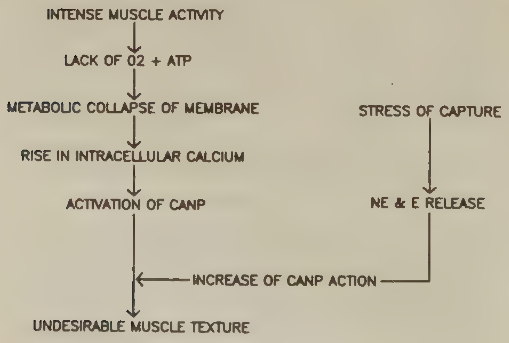

FIGURE 4.—Comprehensive theory of the etiology of burnt tuna proposed in this paper.

The gills are the organ primarily responsible for the degradation of catecholamines, and circulating catecholamines are rapidly cleared from the blood (Nekvasil and Olson 1986). We estimate circulating catecholamines in tuna have a half-life of 30 minutes or less. Therefore, we hypothesize that, in a longline-caught fish remaining in the water for several hours after hooking (Davie and Sparksman 1986), plasma catecholamines are reduced to low levels before the fish is landed and killed, thus resulting in a low percentage of burnt fish. Similarly, fish caught by rod and reel or by handline and fought for several hours would have the low circulating catecholamine levels and low propensity to become burnt. Indeed, Gibson (1981) recommends that handline-caught fish be attached to a buoy and left for an hour prior to being brought on board and killed, as a measure to prevent burnt tuna. That this technique presumably lowers blood catecholamine levels prior to death could explain its efficacy. On the other hand, we hypothesize that a fish landed during the peak of its blood catecholamine concentrations would have the greatest propensity for becoming burnt. This indeed appears to be the case.

The mechanism that ties catecholamines to the observed seasonality and increased number of female fish becoming burnt lies in the biochemical structural similarity of catecholamines and reproductive steroids, particularly estrogen. These steroids reach a peak during spawning season, which is May through October for yellowfin tuna in Hawaii (June 1960). A corresponding increase occurs in the percentage of the tuna catch that becomes burnt during this season (Fig. 3). In the presence of tyrosine hydroxylase, estrogen is converted to catecholestrogen and consequently competes for the same degradative enzymes in the gills, therefore slowing the clearance of catecholamines from the blood (Nekvasil and Olson 1986). Female fish, with high circulating estrogen levels, would then be expected either to reach higher maximum circulating catecholamine levels or to maintain high levels for longer periods, thus explaining the greater number of female fish that become burnt and the seasonality of the occurrence of burnt tuna.

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[8] Although cortisol is also known to be released during stress, its mechanism of action is much slower than NE or E, making it unlikely that it could exert catabolic effects within 15 minutes.

As pointed out by Davie and Sparksman (1986) and Hochachka and Brill (1987), burnt tuna is a quantitative change in tissue decomposition, not a qualitative one. High blood catecholamine levels at the time of death act as accelerators in this inevitable metabolic cascade. However, because we are dealing with a change in rate, the action of catalysts can make all the difference as to whether or not a fish becomes burnt due to CANP.

FUTURE RESEARCH

Under normal conditions, CANP is inhibited by calpastatins. This class of proteins is distinct from the other cysteine protease inhibitors, the cystatins. Although the cystatins can inhibit cathepsins B and H, they are unable to alter CANP activity. Conversely, calpastatin is only effective against calcium-activated neutral protease (Barrett et al. 1986; Parkes 1986). Unfortunately, almost nothing else is known about the relationship of CANP to its endogenous inhibitor, either structurally or physiologically. Certainly investigations into the role of calpastatin would prove valuable for this research.

Immediate future research will concentrate on tracking the specific action of CANP in burnt tuna and attempting to stop this action with Ca^{++} chelating agents such as EGTA (ethyleneglycol-bis-(aminoethyl ether)-N,N,N′,N′-tetraacetic acid) or by use of its intracellular inhibitor, calpastatin. Also, blood catecholamine levels of stressed and unstressed fish will be measured, along with metabolic clearance rates of norepinephrine and epinephrine.

When viewed as a process of metabolic deregulation of CANP, the rapid deterioration of tuna muscle ceases to be an isolated muscular phenomenon. The Z-disc disintegration characteristic of burnt tuna is also present in cardiac muscle injury due to ischemia and muscular dystrophy (Sugita et al. 1984). Given the highly conserved nature of muscle tissue, an understanding of burnt tuna may also provide insights into the metabolic processes of human disease.

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Organ blood flow haemodynamics and metabolism of the albacore tuna *Thunnus alalunga* (Bonnaterre)

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Summary. Metabolic haemodynamic, and organ blood flow measurements were made in tabled, partially anaesthetized albacore *Thunnus alalunga.* Heart rates were 115±9 beats/min: blood pressure 98/75 mm Hg (systolic/diastolic): cardiac output 36.1±5 (ml/min/kg): oxygen consumption 3.4±0.7 (ml O_2/min/kg) and cardiac contractility (dP/dt) 6342±822 mm Hg/s. Organ blood flows were measured with radiolabelled microspheres. The red muscle, kidney, and spleen received the highest flows and the white-muscle the least. There was a flow gradient in the white-muscle with the inner portion near the red-muscle receiving the highest flows. Arterial and venous blood gas measurements showed a reverse temperature effect on arterial PO_2 and a P_{50} of 15.9 Torr corrected to 37° C. Red-muscle temperature was 7° C higher than ambient water temperature. These measurements record the albacore's markedly high cardiovascular capability.

Key words: *Thunnus alalunga* – Oxygen consumption – Blood gases – Organ blood flow haemodynamics

Introduction

There is a paucity of cardiovascular data published for tunas and other scombrid fishes. In this paper we report measurements of cardiac output, quantitative organ blood flow, blood pressures, heart rate, oxygen consumption ($\dot{V}O_2$), blood gases, and core body temperatures for the albacore *(Thunnus alalunga).* Measurements of organ blood flow, haemodynamics and oxygen consumption have rarely been reported for any fish. The organ blood flow data are also notable in that the only other quantitative measurement published for any fish is for rainbow trout (Neumann et al. 1983). Other blood flow determinations were either derived (Cameron 1975) or estimates of relative distribution (Kent et al. 1973; Stevens 1968).

Albacore are endothermic, and by means of a counter current heat exchanger, maintain their deep muscle temperatures up to 10° C warmer than ambient sea water (Carey and Teal 1966; Graham and Dickson 1981). Albacore are also different from most other teleosts in having a high blood volume (Laurs et al. 1978), high haematocrit (Alexander et al. 1980), high metabolic rate (Graham and Laurs 1982), high cardiac performances (Breisch et al. 1983; Lai et al. 1987), specialized haemoglobin-oxygen dissociation characteristics (Cech et al. 1984), and adaptions for continuous fast swimming (Dotson 1976). The present study was undertaken to determine physiological performance levels of albacore.

Materials and methods

Capture, preparation, heart rate, and blood pressure measurements

Studies were conducted at sea on three research cruises aboard the NOAA R/V David Starr Jordan during September 1978, July 1979, and August 1980. Fish were caught by trolling or by rod-and-reel fishing when the ship was stopped. Immediately after a strike the ship was put out of gear and the fish brought along the side of the ship using a hydraulic reel. A dip net was then

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used to bring the fish on board. The time required to land fish caught by trolling was usually about 1 min and to land fish caught by rod-and-reel was 5–15 min. Once aboard, a running sea water hose was placed in the mouth to irrigate the gills while the fish was immobilized by intracardiac injections of gallamine triethiodide (1–2 mg) and immdiately placed in a holding tank. In four fish, tricaine metasulphonate (MS 222) at a concentration of 25 ppm was used to induce anaesthesia, followed by recirculation of MS 222 at 15 ppm for 30 min. No additional anaesthetics were used, so that by the time the first blood pressure and cardiac output measurements were made, some tail movement had returned. Oxygenated sea water was forced past the gills of all experimental fish at a sufficient rate to maintain arterial PO_2 near 60 Torr as determined by measurement of blood gas concentrations with a IL Blood Gas Analyzer, Model 213. The fish were placed in a lateral position during implantation of catheters and flow transducers. Thereafter, the fish were upright in a normal swimming position and submerged in sea water. Organ blood flows and cardiac output were measured in four fish on the 1978 trip. $\dot{V}O_2$ (7 fish), cardiac output (10 fish), haemodynamic parameters, and blood gas levels (18 fish) were measured on the 1979 trip, and effects of temperatures on blood gases (4 fish) and blood P_{50} (4 fish) were measured on the 1980 trip.

Catheters were implanted by removing a small skin flap over the subcutaneous artery and vein just caudal to the pectoral fin. The catheters were passed cephalad, as far as possible, via cutdowns in both the subcutaneous artery and vein. The venous catheter tip was located at the conjecture of the sinus venous and the atrium. The arterial catheter was advanced to the proximal portion of the dorsal aorta (Fig. 1) near the efferent branchial artery. This catheter was used to measure dorsal aortic blood pressure with a Statham P23DB transducer, remove samples for arterial blood gas determinations, inject tracer-labelled microspheres, and withdraw arterial blood samples for determination of cardiac output by dye dilution. The venous catheter was used to obtain samples for blood gas analysis and the injection of dye for cardiac output determination.

Blood pressure measurements were also made in the ventricle and bulbus arteriosus percutaneously with a 19 gauge needle connected to a Statham P23DB transducer. Heart rates were determined from phasic blood pressure measurements in the ventricle, dorsal aorta, and bulbus arteriosus for periods of up to 2 h after instrumentation. A measure of myocardial contractile function, dP/dt (mm Hg/s) of the heart was measured from the slope of the ventricular pressure traces at paper speeds of 100 mm/s.

Cardiac output measurements

Cardiac output measurements were made with an electromagnetic flowmeter (Biotronix, Model 610) in six fish, by dye dilution in four albacore, and with both methods simultaneously in one fish. Dye dilution was used to measure cardiac output in four fish where organ blood flow was determined. The flow transducers were placed around the ventral aorta which was dissected free just anterior to the bulbus arteriosus. In order to avoid occlusion of the coronary artery, which runs along the ventral aorta, the flow transducer (usually 4 mm internal diameter) was fitted around the vessel with the open key slot over the coronary artery. The dye dilution technique was similar to that used by Murdaugh et al. (1965).

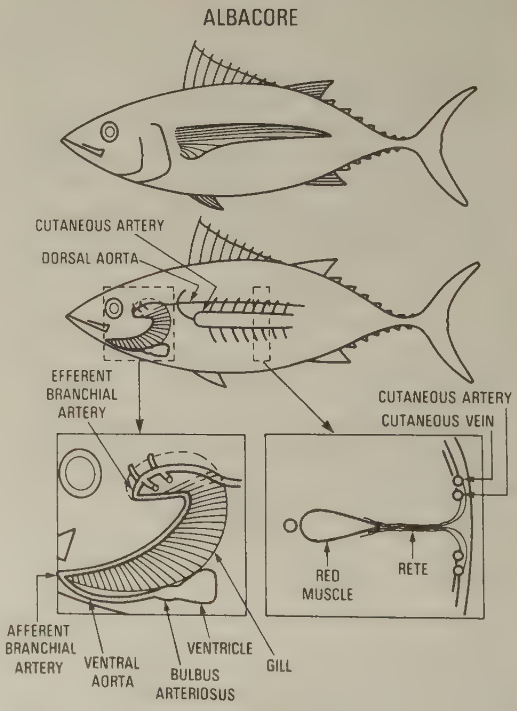

Fig. 1. Relative positions of the cutaneous arteries, veins, retia, heart, dorsal aortic and gills in *Thunnus alalunga*. The *left insert* shows the position of the efferent branchial artery where the tip of the arterial catheter would be positioned. The *right insert* shows the relative position of the red muscle, rete and cutaneous arteries and veins

The dye was injected into the subcutaneous vein and blood was withdrawn from the dorsal aorta. The electromagnetic flow meter technique in fish has been previously described by Johansen (1962).

Organ blood flow measurements

Organ blood flows were determined using tracer-labelled microspheres (^{141}Ce) injected into the dorsal aorta in four albacore showing spontaneous tail movement. Microspheres (15 ± 1 μm in diameter, New England Nuclear, Boston, Mass, USA) were suspended in 10% dextran with a small amount of Tween-80 detergent (0.05%) added to reduce clumping. The accuracy of blood flow measurements determined by microspheres is dependent on having a minimum of several hundred spheres per sample (Heymann et al. 1977). Neumann et al. (1983) found that fish white-muscle is sparsely perfused. We thus injected 2×10^6 microspheres into each albacore to be sure that white-muscle flow estimations could be made.

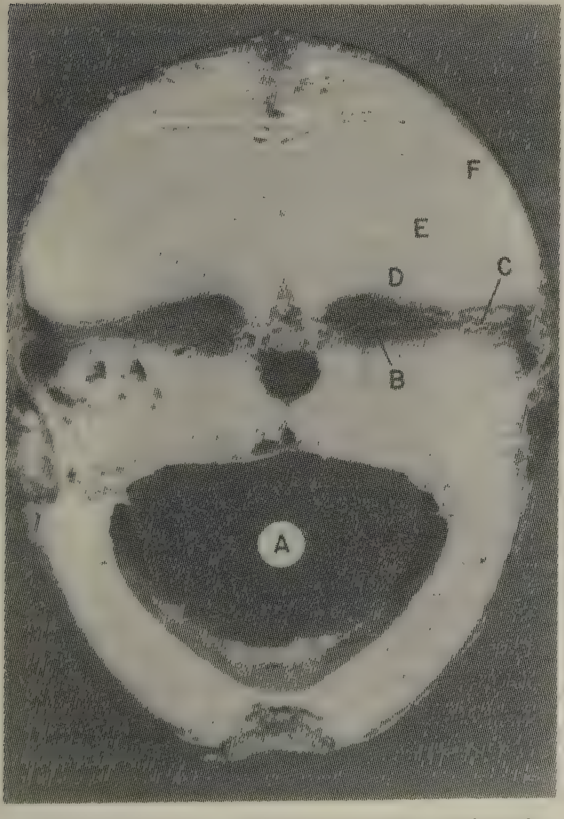

Fig. 2. Relative positions of white- and red-muscle from the midsection of the albacore tuna. *A* body cavity; *B* red-muscle; *C* rete; *D* inner white-muscle; *E* middle white-muscle; *F* outer white-muscle. *D, E* and *F* indicate sites of white-muscle sampling for blood flow measurements

The cardiac output and organ blood flow studies were carried out between 30 min and 1 h after the initial instrumentation. At the end of the experiments, the fish were sacrificed and tissue samples of about 20 g were taken from each organ. These were blotted and weighed, minced, immersed in formalin, and allowed to dry for several days. The pieces were then packed into counting tubes and assayed in a Packard Autogamma Spectrometer (5912A) by standard techniques (Heymann et al. 1977). Blood flow was determined to the red- and white-muscle in samples collected from the side of the fish contralateral to catheter placement. White-muscle samples were taken from the cephalic and caudal sections of the fish and each sample was divided into outer, middle and inner sections (Fig. 2). Red-muscle samples were then taken from the cephalic and caudal areas about the midline of the fish. The entire gill structure was also measured for radioactivity to determine if microspheres had lodged in this tissue. To ensure equal distribution of microspheres to organs of the viscera, the dorsal aortic catheter was inserted as far toward the head as possible (see Fig. 1). At the end of each experiment the position of this catheter was verified. The external diameter of the catheter was 1.0 mm while the internal diameter of the dorsal aorta at this site was about 2.0 mm. Thus sufficient blood flow for normal distribution was available.

The total activity of the microsphere suspension injected into each fish was calculated and regional blood flow was determined as follows:

Tissue flow = (Q × tissue cpm)/(injected cpm) where Q = cardiac output (ml/min), tissue cpm = counts per min in tissue samples, and injected cpm = counts per min of the injected microsphere suspension. Blood flow, expressed as ml/min/g, was computed by dividing tissue flow by the weight of each sample.

Temperature measurements

Needle thermistors were inserted into or near the centres of the red- and white-muscle mass of six fish within 5 min of capture. Temperatures were measured with a Yellow Springs Instrument (YSI), No. 513, thermistor probe and read on a YSI Model 41 Tele Thermometer.

Blood gas measurements were made in 18 fish, 7 of which were also used in $\dot{V}O_2$ studies. The effect of temperature on blood gases was determined by using two gas analysers set at the upper and lower temperature extremes experienced by albacore blood. One instrument (Instrumentation Laboratories, Model 213) was maintained at 22° C (ambient water temperature), while a second (Radiometer Model BMS-3) was set at 32° C, the highest red-muscle temperature likely to be encountered. Blood gas results, used in the $\dot{V}O_2$ calculations, were taken from one machine set at 25° C.

$\dot{V}O_2$ was calculated from the product of cardiac output and arterial-venous O_2 content difference. O_2 contents were calculated as the sum of dissolved plus haemoglobin-bound oxygen. The dissolved O_2 was calculated assuming a blood temperature of 25° C, and a plasma solubility given by the following relationship:
Solubility = 0.00595−0.0001266*T +
0.0000013*T2
where T is the temperature in ° C.

The haemoglobin-bound component was calculated using a standard relationship between tension and partial pressure (Kelman 1966), and using a measured haemoglobin P_{50}. Haemoglobin concentration was measured using the cyanomethaemoglobin technique. To avoid inaccuracies due to interference from erythrocyte nuclei, samples were centrifuged prior to measuring optical absorbance at 540 mn. Haemoglobin P_{50} was measured using a modification of the technique described by Neville (1974). Briefly, 0.1 ml of fresh blood was suspended in 1.6 ml of a yeast-buffer-glucose solution (tris-[hydroxymethyl] aminomethanebuffer,310 m0sm,pH 7.5)andmeasuredby tonometer to a PO_2 of 300−400 Torr. This mixture was injected into a heated cuvette which included a Clark microelectrode fitted with a 0.8 mil polyethylene membrane to improve the response at low levels of PO_2. The mixture was warmed and the fall in PO_2 with time was recorded. The pH of the reacting suspension was measured anaerobically with a glass pH electrode (Radiometer). The P_{50} of the red cells was calculated from the rate of fall in PO_2 with time, and corrected to a pH of 7.4 using a blood gas slide rule (Severinghaus 1966).

Measured and calculated values for all parameters are presented as mean ± standard error of the mean. The student *t*-test was used to determine significance of the mean values between two groups. Differences were considered significant at $P < 0.05$.

Results

Heart rate

Heart rates, calculated from blood pressure measurements, were relatively stable over the 90 min periods of experimentation for each fish (Table 1), but varied considerably among the fishes, (69−150 beats/min). In five albacore a marked drop in heart rate, from 107±3 beats/min to 13±2 beats/min, was noted within 2 min of hypoxia (cessation of ventilation).

Table 1. Heart rate and blood pressure in *Thunnus alalunga*

HR		Ventricular (S/D) (mm Hg)		Bulbus (S/D) (mm Hg)		Dorsal aortic (S/D) (mm Hg)	
Time (min)							
30′	90′	30′	90′	30′	90′	30′	90′
135	133	100/7	55/6	98/75	55/40	78/72	40/38
136	142	112/5	89/4	110/93	75/60	89/85	60/58
76	73	90/8	60/4	90/65	60/36	71/68	45/42
69	73	107/3	105/8	105/80	100/80	96/90	76/72
150	130	90/2	73/5	88/70	70/50	–	–
133	136	100/6	88/5	98/75	–	–	–
120	120	–	89/7	–	–	–	–
136	130	120/10	–	–	–	112/108	70/67
125	95	–	–	–	–	90/84	85/82
136	–	–	–	–	–	68/60	–
120	–	–	–	–	–	–	62/53
142	–	–	–	–	–	77/72	–
$\bar{x}$ 115	115	103/6	79*/6	98/78	72*/53*	84/78	57*/59*
± 5	5	3/1	7/0.05	3/4	8/8	5/5	10/6

S/D Systolic/Diastolic; ± ±SEM (standard error of mean); * Significant $P < 0.05$ compared to 30′; Pressures are given as mm Hg

Table 2. Cardiac output and stroke volume in *Thunnus alalunga*

Fish	Mass (kg)	CO (ml/min)	CO^1 (ml/min/kg)	HR (beats/min)	SV (ml)	Method
1	11.2	320	28.6	99	3.2	DD
2	9.8	340	34.7	120	2.8	DD
3	10.1	362	35.8	142	2.5	DD
4	9.9	280	28.3	79	3.5	DD
4	9.9	273	27.5	82	3.3	EM
5	7.8	374	47.9	104	3.6	EM
6	8.1	194	24.0	89	2.2	EM
7	7.4	458	61.9	77	5.9	EM
$\bar{x}$	9.3	325	36.1	99	3.4	
±SEM (Standard error of mean)	0.5	30	5	8	0.4	

CO Cardiac output; *HR* heart rate at the time of cardiac output measurement; *SV* stroke volume, calculated as $\frac{\mathrm{CO}}{\mathrm{HR}}$;

DD dye dilution; *EM* electromagnetic flow transducer; CO^1 normalized cardiac output $\frac{\mathrm{CO\ (ml/min)}}{\mathrm{Mass\ (kg)}}$

Blood pressures

Systolic and diastolic blood pressures measured in the ventricle, bulbus arteriosus, and dorsal aorta at 30 min and 90 min after the fish were prepared for experimentation, are presented in Table 1. Highest blood pressures were measured in the ventricle during systole, mean 103±3 mm Hg ($n=7$). During diastole there was a marked drop in pressure in the ventricle, mean 6±0.05 mm Hg ($n=7$). Systolic pressures in the bulbus arteriosus, mean 98±3 mm Hg ($n=6$), were almost identical to those in the ventricle, suggesting little pressure drop across the valve. However, bulbus diastolic pressures, mean 78±4 mm Hg ($n=6$), were higher than in the ventricle as would be expected: the former is the true diastolic pressure in the arterial system while the latter is a measure of preload in the ventricle. The mean systolic pressure in the dorsal aorta was 84±5 mm Hg ($n = 8$), which represents an approximate 14% drop in pressure across the gills. During diastole only slight decreases in pressures were recorded in the dorsal aorta, mean 78±5 mm Hg ($n=8$), which is identical to the mean diastolic pressure measured in the bulbus arteriosus.

There was a gradual, but marked decrease in systolic pressures during the experimental period. At 90 min the mean systolic pressures in the ventricle ($n=7$), bulbus arteriosus ($n=5$) and dorsal aorta ($n=7$) were 79±7, 72±8 and 57±10 mm Hg, respectively. These values are significantly lower ($P<0.05$) than those recorded at 30 min. Diastolic pressures in the bulbus arteriosus and dorsal aorta decreased to 53±8 and 59±6 mm Hg, respectively, at 90 min, which are significantly lower ($P<0.05$) than at 30 min. The contractile force of the heart, dP/dt (mm Hg/s), was measured in four albacore at 6342±822 mm Hg/sec.

Cardiac output

Cardiac output data from seven fish are given in Table 2. Fishes 1–4 had cardiac output determined by dye dilution. Electromagnetic flow-transduced cardiac output measurements were made in fish 4–7. Both measurements were made in fish 4 and are in good agreement. Stroke volume showed some variation among fish which could not be accounted for by differences in body mass or heart rate, although there was generally an inverse relationship between heart rate and stroke volume. Cardiac output varied greatly between fish of nearly equal mass, due to differences in heart rate and stroke volume. The mean cardiac output was 36.1±5 (ml/min/kg).

Organ blood flow

Microsphere measurements showed considerable differences in blood flow rates (ml/min/g) to different organs of the body (Table 3). The highest flow was to the kidneys, 0.42±0.07 ml/min/g, and the smallest was to the white-muscle, 0.01±0.005 ml/min/g and to the skin, 0.01±0.005 ml/min/g. Blood flow to white-muscle ranged from 0.029±0.04 ml/min/g (in the inner portion of the fish) to 0.006 ml/min/g (in the midregion of the tail) (Table 4 and Fig. 2). Blood flow measurements as low as 0.003 ml/min/g represent negligible flow and are within the permitted error of the method. Blood flow to red-muscle

Table 3. Organ blood flow in *Thunnus alalunga*

Tissue	Organ Mass (g)	% CO	Flow (ml/min/g)
Red-muscle	452 ± 30	36.2	0.22 ±0.04
White-muscle	5950 ±290	27.5	0.013±0.005
Stomach	136 ± 8	2.8	0.057±0.007
Intestine	28.7± 2	1.8	0.17 ±0.06
Spleen	17.5± 0.5	1.4	0.22 ±0.06
Kidney	45 ± 5	6.7	0.42 ±0.07
Liver	243 ± 16	13.0	0.15 ±0.02
Skin	65 ± 2.1	0.2	0.01 ±0.005

Mean ± SEM (standard error of mean); $N = 4$; Mean body mass = 9.8 ± 0.34 kg; *CO*, cardiac output

Table 4. Regional flow in the white-muscle of *Thunnus alalunga*

	Cephalic	Caudal
Inner	0.029 ±0.04	0.004** ±0.0003
Mid	0.009* ±0.003	0.0006** ±0.0002
Outer	0.004* ±0.006	0.003** ±0.0005

Mean ± SEM (standard error of mean); Flow in ml/min/g; * Significant $P < 0.05$ compared to inner; ** Significant $P < 0.05$ compared to cephalic

Table 6. Oxygen consumption of *Thunnus alalunga*

Fish	Arterial-venous difference (ml O_2/dl)	$\dot{V}O_2$ (ml O_2/min/kg)
1	9.4	2.7
2	12.0	4.2
3	5.6	2.0
4	6.6	1.9
5	9.8	4.7
6	8.4	2.0
7	10.8	6.7
$\bar{x}$	8.9	3.4
±SEM (Standard error of mean)	0.9	0.7

Same fish as Table 2; $\dot{V}O_2$ calculated as: (cardiac output x arterial-venous difference); $\dot{V}O_2$ = oxygen consumption

and spleen were relatively high and identical 0.22±0.04 ml/min/g. Lesser flow rates were recorded to the intestine, 0.17±0.06 ml/min/g, and liver, 0.15±0.02 ml/min/g. A relatively low rate of flow was measured in the stomach, 0.06±0.007 ml/min/g.

Blood gases, oxygen consumption, and body temperature

Blood gas data are contained in Table 5. Arterial PO_2 was 62.0±2.9 Torr and decreased to 14.3±1.2 in venous blood. The arterial blood was significantly more alkaline than the venous blood. Haemoglobin volumes were 15.8±0.1 which is equivalent to a haematocrit of 47.5. Arterial-venous oxygen content difference and oxygen consumptions are given in Table 6. The mean oxygen consumption was 3.4±7 (ml 0_2/min/kg). The effects of temperature on blood gases are given in Table 7. Arterial and venous blood samples from each fish were run at different temperatures in separate blood gas machines. Both arterial and venous blood, had PO_2's which were higher in cooler blood. There was no temperature effect on CO_2 tension but the blood was more alkaline at lower temperatures in both arterial and venous blood. The average P_{50} was 15.9 Torr at a temperature of 37° C and pH of 7.4.

Temperature measurements in red-muscles were made at three time periods: 10–15 min after landing, 30 min, and 90 min. The initial red-mus-

Table 5. Blood gases and O_2 content in *Thunnus alalunga*

Fish	Arterial						Venous				
	PO_2 (Torr)	PCO_2 (Torr)	pH	O_2 Cont (ml O_2/dl)	SAT (%)	Hb (g/dl)	PO_2 (Torr)	PCO_2 (Torr)	pH	O_2 Cont (ml O_2/dl)	SAT (%)
1	68.1	5.6	7.846	21.9	99.4	16.0	14.5	10.5	7.479	12.5	56.9
2	57.5	4.9	7.533	21.7	98.6	15.5	12.1	10.0	7.444	9.7	44.4
3	56.2	3.5	8.038	21.9	99.4	15.4	18.2	6.5	7.522	16.3	74.5
4	70.0	3.8	7.850	22.0	99.5	16.1	17.9	11.9	7.498	15.4	70.4
5	50.5	3.2	7.944	21.4	99.2	15.4	11.3	7.6	7.690	11.6	54.4
6	70.6	3.0	7.807	21.5	99.5	15.7	16.0	10.0	7.440	13.1	60.7
7	61.4	5.0	7.964	21.5	99.4	16.2	9.8	6.6	7.748	10.7	49.9
$\bar{x}$	62.0	4.1	7.855	21.7	99.3	15.8	14.3	9.0	7.546	12.8	58.7
±SEM (standard error of mean)	2.9	0.4	0.62	0.1	0.1	0.1	1.2*	0.8*	0.046*	0.9*	4.1*

Temperature 25° C; *O_2* Content in ml *O_2* per deciliter of blood; *SAT* saturation in %; *Hb* haemoglobin in grams per deciliter; Gas tension in Torr; * Significant $P < 0.05$ venous compared to arterial values

Table 7. Effects of temperature °C on blood gases of *Thunnus alalunga*

Fish	PO_2 (Torr)				PCO_2 (Torr)				pH			
	A		V		A		V		A		V	
	32°	22°	32°	22°	32°	22°	32°	22°	32°	22°	32°	22°
1	39.5	52.6	17.2	18.7	3.0	3.0	5.6	5.6	7.73	8.03	7.55	7.84
2	60.0	67.6	12.2	13.2	2.6	2.6	4.5	8.8	7.55	7.86	7.29	7.49
3	40.0	58.7	6.0	8.1	4.4	4.4	3.2	5.0	7.65	8.02	7.76	7.96
4	26.0	30.1	7.3	7.6	3.3	3.3	10.0	5.8	7.57	7.85	7.57	7.85
$\bar{x}$	41.4	52.3	10.7	11.9	3.3	3.3	5.8	6.3	7.63	7.94	7.54	7.79
±SEM (standard error of mean)	7.0	8.0*	2.6	2.6*	0.4	0.4	1.4	0.9	0.04	0.05*	0.10	0.10*

* Significant $P < 0.05$ 22°C vs. 32°C paired *t*-test; *A* arterial; *V* venous; the temperature (°C) of blood gas machine 1 was 22°C and bloodgas machine 2 was 32°C

cle temperature was 28.9° ± 0.8° C, at 30 min, 26.9° ± 0.7° C and at 90 min, 24.7° ± 0.9° C. The water temperature of the holding tank was 21.9° ± 0.1° C and the surface sea water temperature was 21.3° ± 0.1° C.

Discussion

Heart rate and blood pressure

Reported heart rates in fishes usually range from 25–70 beats/min (Randall 1970). The heart rate of swimming salmon has been measured as high as 100 beats/min (Smith et al. 1967). Heart rates in our study had a very wide range (69–150 beats/min), but the albacore, in which only heart rates and blood pressures were measured (Table 1), had mean heart rates of 115 ± 9 beats/min. These heart rates remained relatively constant over several hours despite decreasing red-muscle temperatures and decreasing blood pressures. Temperature, vagal tone and hypoxia all may have a marked influence on the heart rate of fishes (Randall 1970; Stevens 1972). Hypoxia was probably not a major factor in heart rate measurements in most of the albacore because arterial PO_2 was maintained higher than 60 Torr. As in other species, induced acute hypoxia caused bradycardia in five albacore. The heart rates seen in this study are higher than those reported by Stevens (1972) of 70 beats/min in the restrained skipjack tuna. But Stevens also reported a large variation in heart rate during the experiments (46–142 beats/min) which he attributed to differences in vagal tone. Brill (1987) reported heart rates in skipjack and kawakawa of over 200 beats/min under experimental conditions similar to this study.

Our recordings of ventricular pressures of 98 ± 3 mm Hg are higher than that reported in other teleosts (Randall 1970). Randall et al. (1965) reported ventricular pressures in freshwater fish of approximately 40–45 mm Hg, and in the Pacific salmon Robertson et al. (1966) reported ventral aortic pressures of approximately 80 mm Hg. We observed a systolic pressure drop (20 mm Hg) across the gill which is similar to that reported by other investigators (Hanson 1967; Holeton and Randall 1967; Lai et al. 1987). The high heart rates and blood pressures are physiologic evidence of high cardiac performance. The data from this study showed a relatively high contractile force in the heart (over 6000 mm Hg/s). This high contractile force combined with the filling pressure of 6 mm Hg, can take advantage of the Starling effect which would dictate a relatively high stroke volume. It has been shown that increased filling pressure combined with the increased contractile force of the heart contributes to higher stroke volume (White et al. 1987). Normal mammalian measurements of dP/dt in pigs (White et al. 1987) are 2000 mm Hg/s, which increase to about 8000 mm Hg/s during intense exercise. It appears that the albacore ventricular contractile force is equivalent to that of mammals. Breisch et al. (1983) showed that the albacore myocardium is composed of 82% spongy mass and 18% compact myocardium. It is unlikely that only 18% of the myocardium is responsible for the relatively high amount of cardiac work seen in this fish. Therefore, it is probable that the spongy myocardium provides a considerable force for the ejection of blood and the generation of high ventricular pressures. Further investigations of the force generated by the spongy myocardium are needed to understand fish ventricular mechanics.

Cardiac output and oxygen consumption

Both methods of measurement used in this study, dye dilution and the electromagnetic flow transducer, have been used in fish previously. In our experiments, both methods seem comparable: however the dye technique was simpler to use, and the effects of opening the pericardium in order to implant the electromagnetic flow probe around the ventral aorta, could have a deleterious effect on cardiac function (Lai et al. 1987). Resting cardiac outputs have been measured in a number of fish species. Values in the trout range from 18 ml/min/kg (Kiceniuk and Jones 1977) to 45 ml/min/kg (Neumann et al. 1983). Using the electromagnetic flow probe, Johansen (1962) measured a cardiac output of 9.3 ml/min/kg in the cod. Murdaugh et al. (1965), using dye techniques, measured a cardiac output of 26.7 ml/min/kg in *Squalus acanthias.* Our measurements of about 34 ml/min/kg appear to be not unusual for a teleost and are very similar to that reported in the albacore by Lai et al. (1987). But we must be cautious on any interpretation of the cardiac output in a partially anaesthesized and traumatized fish compared to one that is free swimming. $\dot{V}O_2$ data given in this paper are similar to that given by Graham and Laurs (1982) for albacore swimming in a respirometer.

Organ blood flow

The microsphere method allowed several observations to be made about organ blood flow in the albacore. However, this method was limited because of the unavailability of a suitable catheter location to distribute microspheres to the heart and brain. Since both the heart and brain are perfused by arteries coming from the efferent branchial arteries, no microspheres reached these organs. The relative and absolute blood flows to various organs are similar to those reported in the Arctic grayling (Cameron 1975), although the kidney and the spleen flows are somewhat lower and higher respectively. White-muscle blood is sparse but there is a heterogenous flow of blood to this organ. We found that white-muscle blood flow was highest nearest the red-muscle and decreased to near zero in the caudal direction. This is in agreement with the finding of Cameron (1975) that the highest white-muscle flows were in the cephalic direction. These data may support the concept that tuna white-muscle possesses a greater potential for aerobic metabolism, particularly in the region where temperatures are elevated. Graham et al. (1983) suggested that white-muscle activity partiall assumes red-muscle function where the temperatures are elevated. Our finding that the inner white-muscle has increased blood flow further supports the concept of a mixed function and morphology for albacore white-muscle.

Red-muscle received the highest percentage of the total cardiac output, approximately 36%, although this organ represents less than 5% of the fish mass. The rate of blood flow to the white-muscle was quite low, but due to its large mass, occupying more than 60% of the total mass of the fish, the white-muscle received almost 28% of the cardiac output. The liver, which accounts for 2.5% of the total body weight, received 13% of the cardiac output. The kidney, while comprising only 0.5% of the total body weight, received 6.7% of the cardiac output. The stomach received less than 3% of the cardiac output, the intestine and spleen each received less than 2% and the skin less than 0.2%. Our measurements account for 89.6% of the cardiac output. Microspheres in the gills account for another 5% of the total injected. We asume that the remainder, approximately 4.5%, found its way to tissues that were not assayed (bone, heart, brain, and other organs). These tissue blood flows are similar to those found in mammals.

Blood gas measurements

The blood gas measurements presented here are markedly similar to those of Jones et al. (1986) in the free swimming tuna, *Euthynnus affinis* (kawakawa). Cech et al. (1984) clearly showed a reverse temperature effect of lowering arterial PO_2 with warming in the albacore, while Jones et al. (1986) showed a positive temperature effect in the kawakawa. Our data confirm the reverse temperature effect on PO_2 in albacore and show a decrease in pH with increasing temperature. However, we could not see marked temperature effects on CO_2, perhaps because of the narrow range of CO_2 values in the blood. Our P_{50} value of 15.9 Torr is lower than that reported by either Cech et al. (1984) or Jones et al. (1986). However, this value is not unreasonable given that the average venous PO_2 we observed (Table 5) was 14.3 Torr at 25° C

In conclusion these data show that the albacore tuna is capable of relatively high cardiovascular performances and blood flows which are similar to those in mammals.

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Appendix 3

BOWHEAD POPULATION ESTIMATE AND VARIANCE

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As indicated in SC/39/PS7, likely upward bias in the 1986 population size estimates in Table 7 of that paper preclude their use in assessing the size of the stock. Sub-committee discussions have pointed to the estimates 8,778 and 5,641 as the most acceptable estimates among those presented for 1985. Clear sources of bias (for example, the failure to account for unmonitored hours) suggest that the other 1985 estimates in Table 7 should be eliminated.

It would be desirable to have independent evidence that the tracking parameters used produce unbiased counts of whales. Separate studies of bowhead migration behaviour indicate a reasonable range of speed and direction parameters but provide only limited help in setting these parameters for a particular part of a particular season.

We therefore depend on the visual census to guide our choices. The tracking parameters which result in the estimate 8,778 also produce counts of visual tracks which match the observers' counts of new whales plus half the conditional whales. The tracking parameters which produce the estimate of 5,641 result in a somewhat better match between speed and direction distributions computed from tracks and from duplicate sightings made by the visual census.

Thus we cannot be sure which of these estimates is most unbiased. We therefore propose their average (7,200) as our current best estimate of the size of this stock. A jack-knife variance estimate was suggested by Chapman. Such an estimate, conditioned on the assumption that the tracking algorithm counts duplicates correctly, was computed from the data which produced the estimate 5,641. We were not able to compute a variance for the larger estimate because we did not have all the necessary data at this meeting.

The jack-knife variance estimate we use is given by (18) and (19) of Zeh *et al.* (1986, *Rep. int. Whal. Commn* 36: 317–23). We have 35 time periods of varying length with acoustic and/or visual watch in the 1985 season*. We can therefore obtain 35 different population estimates by omitting each period in turn from our calculations. The appropriate average of these provides a variance estimate which reflects the effect of omission of each period on the mark-recapture estimates of whale numbers and detection probabilities, the estimates P_3, and interpolation for unmonitored hours. The estimated standard error obtained by this method is 1,900. We believe this provides a reasonable measure of the variability of the estimate 5,641.

The standard error reported above indicates a coefficient of variation of 34% which we assume is applicable to the mean estimate of 7,200. We therefore propose 7,200 ± 2,400 (where 2,400 is 1SE) as the current best population size estimate.

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* Our 35 time periods take the role of the watched days in equations (18) and (19).

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SURFACE pH, SATELLITE IMAGERY AND VERTICAL MODELS IN THE TROPICAL OCEAN

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ABSTRACT

The relationships between surface pH, ocean color and surface temperature are discussed conceptually. As an example, log pigment and sea-surface temperature (SST) obtained from color and IR satellite imagery collected over the Gulf of California (Mexico) in November 1981 are compared with in situ pH and temperature measurements made 3 weeks later. Plots of log pigment vs. SST and pH vs. in situ temperature show a characteristic break in slope, suggesting that the area studied may be divided into a high productivity northern section and a southern section of correspondingly lower productivity. A multidisciplinary (physical–chemical–biological), one-dimensional (vertical) model is used to produce characteristic shapes of log pigment vs. SST and pH vs. in situ temperature plots.

INTRODUCTION

The development of space-based systems for ocean exploration has presented oceanographers with the opportunity to monitor the ocean's surface synoptically over distances from tens to thousands of kilometers. The two properties most commonly observed with satellites are sea surface temperature (SST) and upwelled color, computed as pigment, which in oceanic waters is a measure of the abundance of phytoplankton in the upper 10–40 m (Gordon et al., 1980, 1983). In tropical waters, the concentration of phytoplankton is related to the quantity of nutrient-rich subsurface water which penetrates the photic zone and the duration of its exposure to solar radiation. Because these latter parameters are controlled by upwelling and turbulent mixing, complex relationships exist between hydrography and satellite-measured temperature and color.

Knowledge of surface–subsurface relationships extends the usefulness of the imagery and provides the theoretical framework for ocean monitoring from space. Such monitoring is much more economical than surveys by ship. At present, data bases for developing algorithms which link subsurface structure to imagery are provided by oceanographic expeditions in which surface (mixed layer) properties are continuously sampled by underway ships as the imagery is collected (Zirino, 1985). Thus, the distances that can be surveyed by the ships

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in a few days approach these covered in the imagery. Ship's surface observations are also augmented with XBT drops and by frequent shallow sampling at discrete stations where full-scale hydrographic measurements (including pH and total carbon dioxide) are performed. Shallow casts can be executed quickly and do not significantly reduce horizontal coverage.

Imagery and sea-truth data may be brought together in multidisciplinary (physical–chemical–biological) simulation models which link the appropriate variables and provide a mechanistic interpretation for both surface and subsurface observations. Because the horizontal features of the surface volume of interest are already present in the imagery, one-dimensional vertical models provide the important link between surface, mixed layer, thermocline and deeper waters. Figure 1 provides an artist's rendition of this approach.

Pigment and surface temperature

In upwelling areas, pigment, or chlorophyll-*a* concentration in the mixed layer computed from upwelled color, has been found to vary non-linearly with sea-surface temperature (Abbott and Zion, 1985). Pigment concentration appears to peak at an optimum temperature and is progressively less at lower and higher temperatures. For example, in waters off the coast of California, Abbott and Zion (1985) found that pigment concentration peaked at ~12°C. The same-shaped plot was observed in October 1985 by Zirino et al. (1988) for a 700 km transect of the Gulf of California, although the pigment maximum occurred at a temperature ~10° higher. The relationship can be explained as a series of states in a temporal upwelling–stratification sequence. Initially, cold, chlorophyll-poor, nutrient-rich water is brought to the surface by upwelling. Solar radiation then heats the water and promotes phytoplankton growth. Growth continues until stratification of the water column and/or advection away from the upwelling site reduce the flux of nutrients into the mixed layer, thereby causing the plankton concentration to decrease while

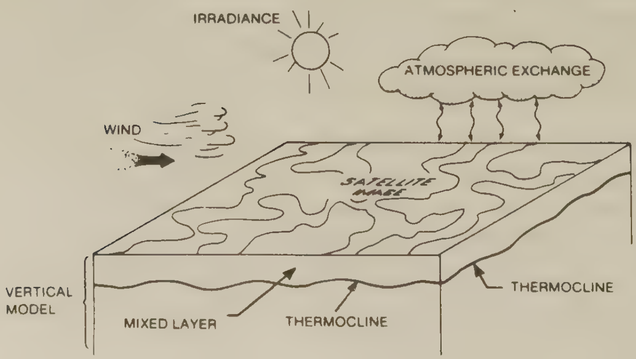

Fig. 1. Artist's conception of satellite imagery as a result of physical forcing.

temperature continues to increase to some steady-state value. This progression of events is shown diagrammatically in Fig. 2A and is presumed to hold for all waters in which stratification is controlled by temperature rather than salinity.

Figure 2A shows that pigment concentration increases exponentially from low to optimum temperatures and then decreases, again exponentially, at higher temperatures. Because of this exponential nature of the growth pattern, log pigment vs. temperature plots resemble the intersection of two straight lines with a sharp bend or "knee" at the intersection (Fig. 2B). In practice, however, the entire left-hand side of the plot is seldom, if ever, observed (new, cold water would need to surface extremely quickly) and the right-hand side of the plot predominates in most images. In a detailed study of northern California coastal waters, Abbott and Zion (1985) found that a relatively linear, inverse, log pigment–SST relationship existed in imagery collected at the site over several days, and they used the relationship to map out areas of positive or negative "anomalies" (higher or lower pigment than predicted by the relationship). Both kinds of anomaly were associated with large plumes streaming from the coast for 200–300 km.

pH, total carbon dioxide (TCO_2) and temperature

The pH of oceanic surface waters contains information which may be related to both temperature and chlorophyll-*a* concentration and thus to SST and pigment in imagery. In tropical waters, or in any waters where the density structure is determined by temperature, pH profiles tend to show the same

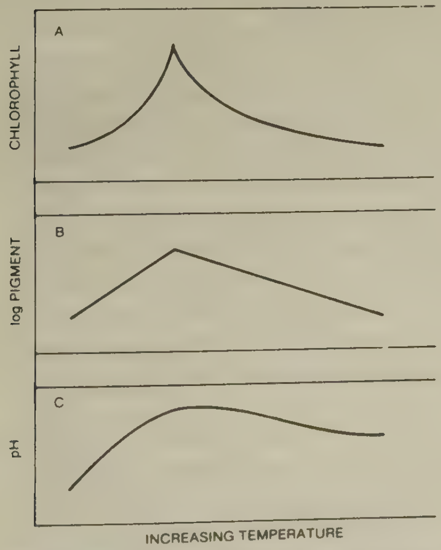

Fig. 2. Diagrammatic representation of chlorophyll concentration, log pigment, and pH at the ocean's surface as a function of increasing surface temperature.

features as temperature profiles (Zirino et al., 1986). Indeed, they are often linearly related, despite the fact that the pH profile contains *both* physical and biological information.

The reason for this is as follows: in the absence of biological processes, the pH of ocean water with a salinity of 34–36 ppt, measured at 1 atm. pressure and 25°C, would be $\sim 8.23 \pm 0.02$ (Zirino et al., 1986). This is the value attained when carbon dioxide gas, carbonic acid, bicarbonate and carbonate ions in the water reach equilibrium with atmospheric CO_2. In the euphotic zone, solar radiation warms the water and simultaneously drives photosynthesis which removes CO_2 and raises the pH, viz.,

$$HCO_3^- \rightarrow CO_2 + OH^- \qquad (1)$$

On the other hand, in colder, aphotic (subsurface) water, respiration releases CO_2 and lowers the pH. Thus, warm surface waters tend to have a high pH, while deeper, colder waters have a $pH < 8.2$. When mixing masks in situ biological processes, temperature, pH, salinity, nutrients, etc., in the upper 100 m can be expected to be linearly related to each other, giving rise to similar (or mirror image) vertical profiles.

However, this covariation is misleading because pH and temperature are not directly related (the effect of temperature on pH in the ocean is small (Zirino et al., 1986)). For instance, there is no a priori reason for the surface water to both heat and increase pH via photosynthesis at a proportional rate. In fact, while mixing processes may be identical for both variables, in situ processes at the end points may be unrelated, with pH and temperature changing within their respective biological and physical constraints.

pH vs. temperature obtained from continuous measurements from underway ships may also produce characteristic plots, somewhat analogous to the pigment vs. temperature plots obtained from satellites. For example, consider the course of a ship from an area of newly upwelled water, through zones of increasing primary production but also progressive stratification, to a terminal area of high stratification and very low production. A plot of surface pH vs. surface temperature values collected on this transect could be represented by Fig. 2C. The lower, left-hand portion of the curve, that representing the "newest" upwelled water, is characterized by the lowest pH value, as well as the lowest temperature. The plot then shows a steep, positive slope as solar radiation heats the water and drives production. Finally, the slope decreases as productivity becomes limited by lack of nutrients, ultimately reaching a plateau where pH no longer increases, although temperature might still continue to increase.

Implicit in this conceptual model (Fig. 2C) are two assumptions: (i) pH is proportional to TCO_2 and changes in pH accurately reflect changes in TCO_2, and (ii) that TCO_2 is essentially conserved in the system, i.e. changes in TCO_2 from loss or gain across the air–sea boundary are small when compared with biologically produced effects. The first assumption appears well justified. Zirino et al. (1986) pointed out that a nearly linear relationship existed between pH and TCO_2 if the specific alkalinity was held relatively constant. During the GEOSECS expeditions (Broecker et al., 1982) it was found that the specific alkalinity of Pacific surface waters was essentially constant at ~ 0.1197 and therefore pH and salinity could be used to predict TCO_2 to within $\pm 8\,\mu M\,\mathrm{kg}^{-1}$. While specific alkalinity in Atlantic surface waters was slightly more variable, TCO_2 could still be predicted from pH and salinity with high accuracy. Our own measurements in the North Atlantic and in the Gulf of California in 1985 substantiate this observation (Zirino et al., 1988).

The second assumption also appears to be justified. The velocity with which $CO_2(g)$ exchanges across the air–sea boundary is approximately ten times smaller than that of other gases in seawater. Broecker and Peng (1982) estimate that ~ 1 year is required for $CO_2(g)$ in the upper 50 m to reach atmospheric equilibrium. This period is much longer than the time required for a biological response to atmospheric forcing which occurs in periods of days or weeks. Since biological CO_2 changes are directly correlated with pH changes, it follows that the pH of surface water is often different from the "equilibrium pH" and much more indicative of in situ biological processes. It also follows that, because atmospheric exchange is slow, the pH of the surface water represents an integral of individual photosynthesis or respiration events occurring over days, weeks or, perhaps, months.

This is not to say that there is no $CO_2(g)$ exchange across the air–sea boundary, but that $CO_2(g)$ loss or gain to the atmosphere must be considered as part of a TCO_2 budget in which, generally, biological processes cause the greatest changes. Of course, where production is low, air–sea exchange becomes a significant if not predominant component of the CO_2 budget.

Multidisciplinary vertical models

The complex relationships between physical, biological and chemical variables observed in the field can be better understood by means of models which simulate the important time-dependent processes occurring in the oceans. Such models are driven by physical forces (solar radiation, winds, currents) which cause biological responses (photosynthesis, grazing) which, in turn, result in measurable chemical and biological changes (nutrients, chlorophyll, oxygen, CO_2). Unfortunately, while there are excellent working models in each discipline, there is, at present, no commonly accepted multidisciplinary vertical model.

The desire to understand better the interactions among common oceanographic variables at and near the ocean's surface led us to develop a relatively simple, multidisciplinary, vertical model which incorporates many of the features found in the single discipline models. The model is of the differential type, in the sense that the equations for heat, momentum, plankton, nutrients (nitrogen), oxygen and CO_2 are not integrated over the mixed layer. Rather, the surface layer is simulated by an arbitrary number of discrete layers with variable diffusivities between them. This type of model allows for high vertical resolution, compatible with the resolution presently available with pump profiles of temperature, pH and chlorophyll (Fuhrmann and Zirino, 1988).

We have used the vertical model to understand better the shapes of pigment and pH vs. temperature plots for the Gulf of California. These plots were obtained from satellite imagery and horizontal transects sampled at sea during the Naval Ocean Systems Center's VARIFRONT III expedition to the Gulf of California during Nov.–Dec. 1981. This report presents and discusses our findings.

METHODS

Data collected at sea

pH and temperature measurements were made aboard the USNS deSteiguer on 10–11 December 1981. Water was obtained from a hull penetration in the scientific sea chest, ~ 3 m below the water's surface, and pumped into the ship's laboratory. pH, temperature and chlorophyll were measured continuously during the transect as described in Zirino and Lieberman (1985) and Lieberman et al. (1987). pH at 25°C was computed from the mV readings of the glass electrode and the temperature readings of the adjoining thermistor (Zirino and Lieberman, 1985).

Imagery

Color and thermal images were collected at the Scripps Satellite Oceanographic Facility (SSOF) of the Scripps Institution of Oceanography in La Jolla, California, on 16 and 17 November 1981, and archived and processed thereafter. Daytime thermal infrared data from channel 4 ($11\,\mu$m) of the Advanced Very High Resolution Radiometer (AVHRR) on the NOAA-7 satellite were corrected for the effect of thin low clouds, using channel 2 (0.7–$1.1\,\mu$m) near-infrared data (Gower, 1985), and then calibrated by an SSOF radiometric calibration procedure based on Lauritson et al. (1979). Multi-channel correction for absorption of sea-surface radiance by atmospheric water vapor was not employed because preserving the better signal-to-noise ratio of the single-channel data was more important than an accurate temperature estimate. Visible radiance data from the Coastal Zone Color Scanner (CZCS, on the Nimbus-7 satellite) were processed with an algorithm based on Gordon et al. (1983) to remove effects of Rayleigh and aerosol scattering and to derive pigment concentrations from corrected blue/green ratios.

Model

In the vertical model (Keir and Fiedler, 1988), heat and momentum are input by solar radiation and surface wind stress. Solar radiation is attenuated at depth as a function of phytoplankton pigment concentration. Heat loss from the surface is a linear function of surface temperature. Nitrate flux is determined by upwelling and turbulent mixing. Phytoplankton growth is a function of light intensity, nitrate concentration and phytoplankton biomass. Light attenuation varies with phytoplankton biomass. Turbulent mixing is modeled as the product of the vertical gradient of a property and an eddy diffusion coefficient. Eddy diffusivity varies as a function of the gradient Richardson number (stratification/shear, Paconowski and Philander, 1981). Diffusion of oxygen and CO_2 through the sea surface is represented by the stagnant film model (Liss, 1975). Grazing is assumed to be a constant fraction of phytoplankton carbon per unit time. Phytoplankton grazed at a particular depth is redistributed at depth according to an exponential function, and remineralized, utilizing oxygen. Changes in carbon, oxygen, and nitrogen are linked by the Redfield ratio (Redfield et al., 1963).

A set of non-linear, partial differential equations represents conservation of mass, momentum and heat in the system. The Crank–Nicholson method is used to solve the set of equations in discrete form. The resulting set of algebraic equations takes on a tri-diagonal matrix form and the solution converges in one to three iterations at each time step. The user specifies the number of depth intervals and total depth of the water column to be modeled, as well as the time step, in days, for solution of the discrete equations. Initial concentrations of the variables upwelling velocity, surface wind speed, and surface light intensity are the inputs required at the start of a model run. The code is in QUICK BASIC and runs on an IBM personal computer or compatible instrument.

RESULTS AND DISCUSSION

Figure 3A,B shows the processed SST and pigment images of the Gulf obtained from satellite data collected on November 16 and 17. Temperature decreases and pigment concentration increases with degree of whiteness. The line leading from north to south approximates the track of the USNS DeSteiguer 24 days later. From the southern portion of the basin to just south of the two major islands, the IR image displays progressively colder temperatures, with the coldest water occurring southwest of Tiburon Island, where the topography shoals from a depth of ~ 1800 to 200 m. This zone of cold water persists throughout the year and coincides with the boundary between the shallow, northern region of ~ 200 m depth, and a deeper southern region (Fig. 4). Four major basins of progressively increasing depth (Guaymas, Carmen, Farallon and Pescadero) are sequentially located along the length of the southern Gulf.

Intense forcing by tides, winds, solar heating and exchanges with the Pacific Ocean promote a vigorous circulation, characterized in the south by large, deep, eddies and wind-driven coastal upwelling. Plumes of upwelled water

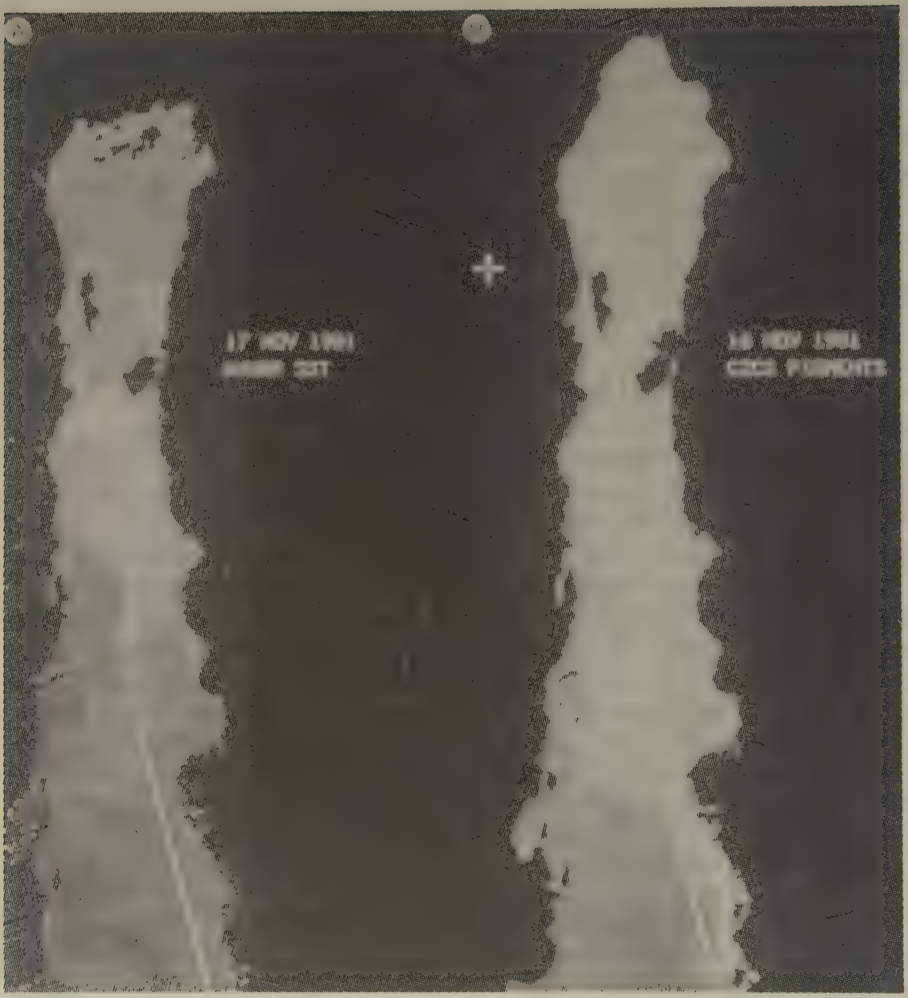

Fig. 3. Satellite imagery of sea-surface temperature (SST) and color imagery of the Gulf of California, Nov. 16–17, 1981.

stream from the coasts along the boundaries of the eddies. The direction of rotation of the eddies as well as the location of coastal upwelling (east, west) varies seasonally with the direction of the prevailing winds.

Figure 3A shows features typical of the surface thermal structure of late fall, winter and early spring (Badan-Dangon et al., 1985). This structure is notable for large, anticyclonic eddies extending across the Gulf in the Guaymas and Carmen Basins. Driven by a northwesterly wind, cold water upwells along the east coast and streams across the Gulf. On November 17, the coldest water (~ 19°C) was found south of Tuburon Island, streaming towards the west coast and forming the northern boundary of the Guaymas eddy. The eddy itself is

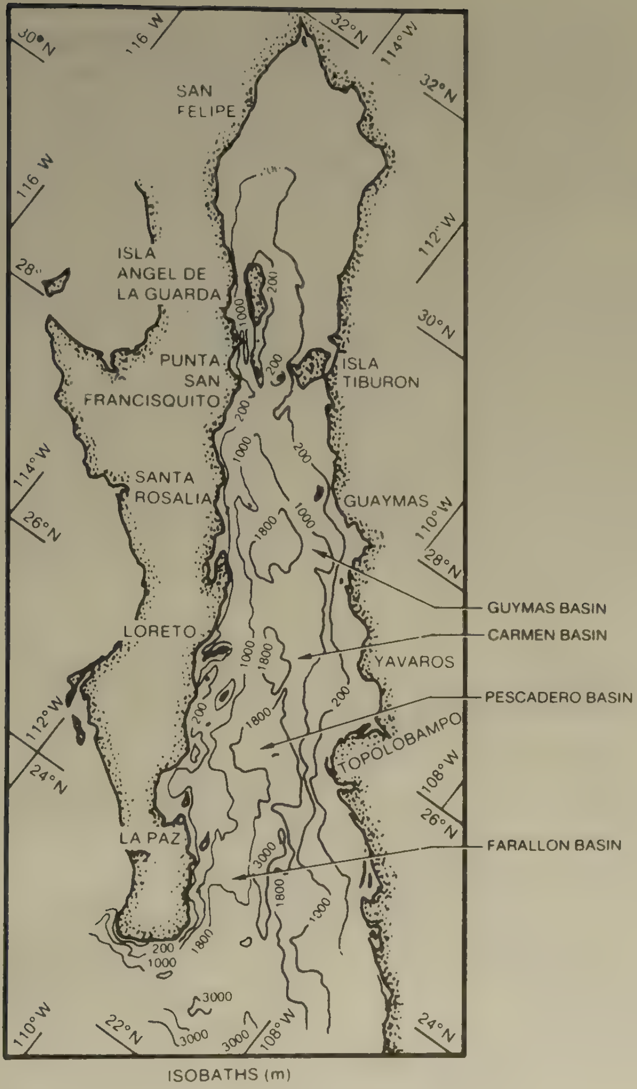
30°N
116°W
32°N
114°W
32°N
SAN FELIPE
116°W
112°W
ISLA ANGEL DE LA GUARDA
28°
30°N
PUNTA SAN FRANCISQUITO
ISLA TIBURON
114°W
SANTA ROSALIA
GUAYMAS
110°W
26°N
28°N
GUYMAS BASIN
CARMEN BASIN
LORETO
YAVAROS
PESCADERO BASIN
112°W
TOPOLOBAMPO
108°W
24°N
26°N
LA PAZ
FARALLON BASIN
200
1000
1800
3000
110°W
22°N
108°W
24°N
ISOBATHS (m)

Fig. 4. Bathymetric chart of the Gulf of California.

split into two smaller eddies separated by a plume of 20.5°C water which emanates north of Guaymas and reaches west to Santa Rosalia. The southern boundary of the eddy is marked by a plume of ~22°C water which leaves the coast just south of Guaymas, reaches the center of the Gulf and then deflects southward to form a small cyclonic gyre. Several such small (~30–50 km) eddies mark the surface waters of the Carmen Basin, which have a mean temperature of ~23°C and which are separated from more southerly waters by a steep 1°C front radiating westward of Topolobampo.

The pigment image, Fig. 3B, shows spatial structure similar to that found in the IR image, although the pattern is less intense. A major difference is a 10 km wide, high-pigment zone which hugs the mainland coast. This zone, which has no temperature counterpart, is also found in 1985 Gulf imagery (Zirino et al., 1988). From south to north, pigment increases by about an order of magnitude, but this is somewhat obscured in the image which, as customary, is log-transformed.

Figure 5A displays log(pigment) along the north–south cruise track shown in Fig. 3. Pigment values range from $\sim 0.3\,\mu g\ l^{-1}$ in the south to $\sim 3\,\mu g\ l^{-1}$ in the north. Similarly, Fig. 5B displays SST along the same path. Figures 5C and D display the in-situ "surface" (actually 5 m) pH and temperature measured along the track on December 10–11, 3.5 weeks later. For comparison, the graphs have been drawn to the same horizontal scale. It is evident from the temperature plots that, despite some shifts in the relative positions of the eddies, the locations and temperatures of major features in the Gulf remained relatively unchanged during the 3.5 week period between the two data sets. While there is roughly a one degree absolute difference between the sets, they

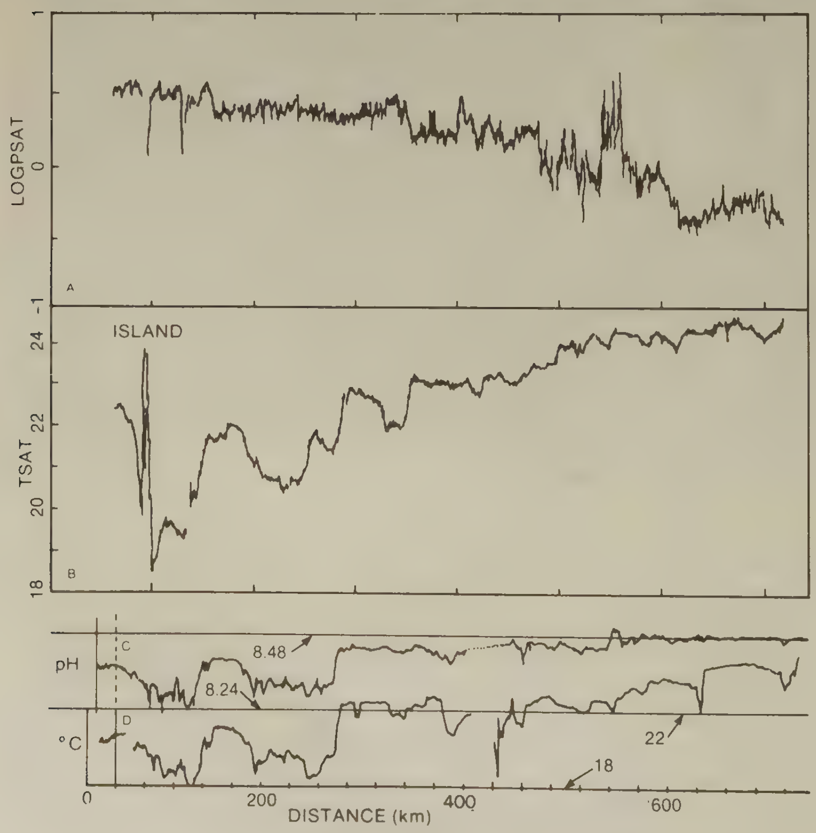

Fig. 5. Log pigment, SST, pH and in situ temperature of the Gulf of California, Nov.–Dec. 1981.

are in fact highly correlated, and a one degree difference between two such diverse measurements is not unexpected.

Figure 6(A,B) shows plots of log pigment vs. SST and pH vs. "surface" temperature measured at sea. In both plots there is a major change in slope occurring at ~22°C. This temperature marks the southern boundary of the eddy which occupies the Guaymas Basin and divides the Gulf into a high-pigment northern region and into a southern area of progressively lower pigment (and chlorophyll). pH is low in the high pigment region, increasing at a relatively rapid rate to ~8.47 and then leveling off at this value, in the southern, low-pigment zone. Zirino and Lieberman (1985) suggested that the

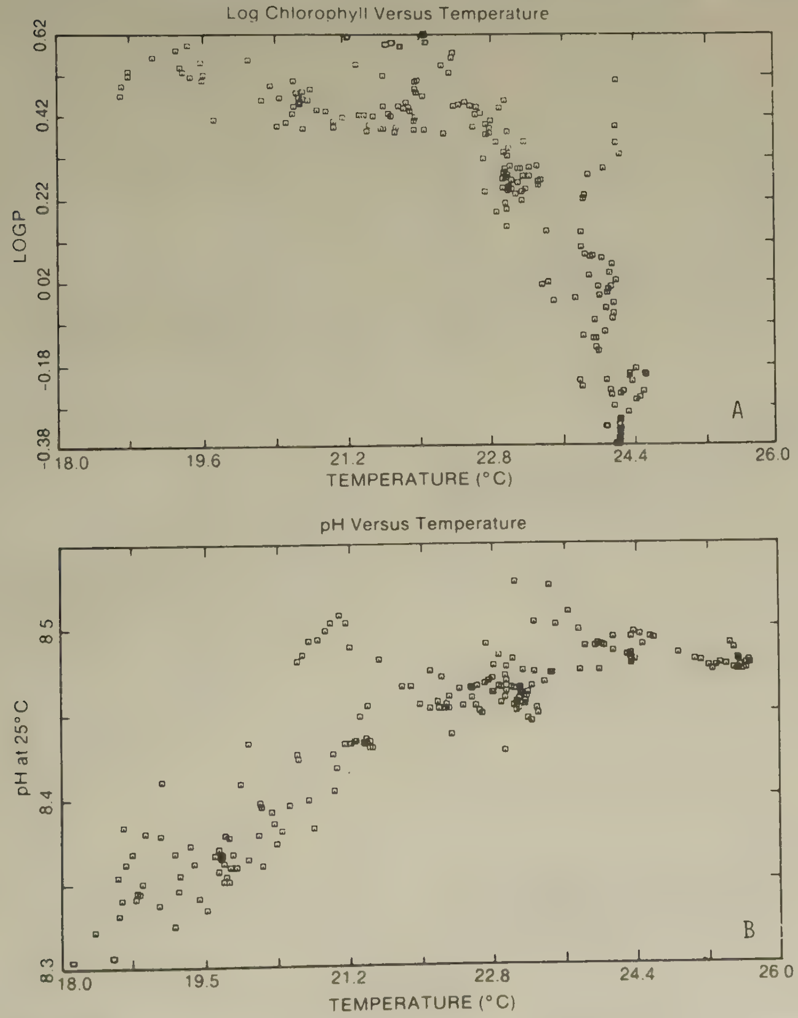

Fig. 6. (A) Log pigment vs. SST and (B) pH vs. in situ temperature. Gulf of California, Nov.–Dec. 1981.

increase in pH in the northerly region was the result of high primary production. Indeed, Baumgartner (1988) pointed out that, in the Gulf, primary production and chlorophyll concentration were linearly related.

The clear "break" in both plots at ~ 22°C suggests that log pigment and pH are related to temperature in the manner discussed earlier (Fig. 2) and that two different productivity regimes exist within the 800 km transect studied. It is not particularly clear, however, how the rate of change of chlorophyll standing stock with temperature relates quantitatively to the rate of change of pH or TCO_2 with temperature, since we did not measure any rates. Instead, the relationship between the two data sets was studied by means of the vertical model which relates all the time-dependent variables quantitatively.

Vertical model

Figure 7 shows time–depth plots of two runs of the model with 10 m layers

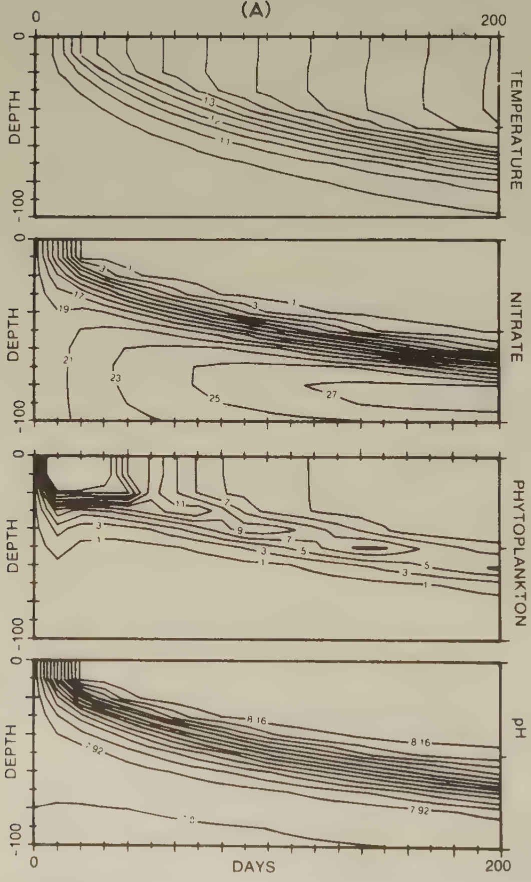

Fig. 7. Time–depth plots of model simulation. (A) Low mixing: upwelling = 0 m day^{-1}, winds = 2 m s^{-1}. (B) High mixing: upwelling = 0.5 m day^{-1}, winds = 5 m s^{-1}.

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Organ blood flow haemodynamics and metabolism of the albacore tuna *Thunnus alalunga* (Bonnaterre)

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Summary. Metabolic haemodynamic, and organ blood flow measurements were made in tabled, partially anaesthetized albacore *Thunnus alalunga.* Heart rates were 115±9 beats/min: blood pressure 98/75 mm Hg (systolic/diastolic): cardiac output 36.1±5 (ml/min/kg): oxygen consumption 3.4±0.7 (ml O_2/min/kg) and cardiac contractility (dP/dt) 6342±822 mm Hg/s. Organ blood flows were measured with radiolabelled microspheres. The red muscle, kidney, and spleen received the highest flows and the white-muscle the least. There was a flow gradient in the white-muscle with the inner portion near the red-muscle receiving the highest flows. Arterial and venous blood gas measurements showed a reverse temperature effect on arterial PO_2 and a P_{50} of 15.9 Torr corrected to 37° C. Red-muscle temperature was 7° C higher than ambient water temperature. These measurements record the albacore's markedly high cardiovascular capability.

Key words: *Thunnus alalunga* – Oxygen consumption – Blood gases – Organ blood flow haemodynamics

Introduction

There is a paucity of cardiovascular data published for tunas and other scombrid fishes. In this paper we report measurements of cardiac output, quantitative organ blood flow, blood pressures, heart rate, oxygen consumption ($\dot{V}O_2$), blood gases, and core body temperatures for the albacore *(Thunnus alalunga).* Measurements of organ blood flow, haemodynamics and oxygen consumption have rarely been reported for any fish. The organ blood flow data are also notable in that the only other quantitative measurement published for any fish is for rainbow trout (Neumann et al. 1983). Other blood flow determinations were either derived (Cameron 1975) or estimates of relative distribution (Kent et al. 1973; Stevens 1968).

Albacore are endothermic, and by means of a counter current heat exchanger, maintain their deep muscle temperatures up to 10° C warmer than ambient sea water (Carey and Teal 1966; Graham and Dickson 1981). Albacore are also different from most other teleosts in having a high blood volume (Laurs et al. 1978), high haematocrit (Alexander et al. 1980), high metabolic rate (Graham and Laurs 1982), high cardiac performances (Breisch et al. 1983; Lai et al. 1987), specialized haemoglobin-oxygen dissociation characteristics (Cech et al. 1984), and adaptions for continuous fast swimming (Dotson 1976). The present study was undertaken to determine physiological performance levels of albacore.

Materials and methods

Capture, preparation, heart rate, and blood pressure measurements

Studies were conducted at sea on three research cruises aboard the NOAA R/V David Starr Jordan during September 1978, July 1979, and August 1980. Fish were caught by trolling or by rod-and-reel fishing when the ship was stopped. Immediately after a strike the ship was put out of gear and the fish brought along the side of the ship using a hydraulic reel. A dip net was then

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used to bring the fish on board. The time required to land fish caught by trolling was usually about 1 min and to land fish caught by rod-and-reel was 5–15 min. Once aboard, a running sea water hose was placed in the mouth to irrigate the gills while the fish was immobilized by intracardiac injections of gallamine triethiodide (1–2 mg) and immdiately placed in a holding tank. In four fish, tricaine metasulphonate (MS 222) at a concentration of 25 ppm was used to induce anaesthesia, followed by recirculation of MS 222 at 15 ppm for 30 min. No additional anaesthetics were used, so that by the time the first blood pressure and cardiac output measurements were made, some tail movement had returned. Oxygenated sea water was forced past the gills of all experimental fish at a sufficient rate to maintain arterial PO_2 near 60 Torr as determined by measurement of blood gas concentrations with a IL Blood Gas Analyzer, Model 213. The fish were placed in a lateral position during implantation of catheters and flow transducers. Thereafter, the fish were upright in a normal swimming position and submerged in sea water. Organ blood flows and cardiac output were measured in four fish on the 1978 trip. $\dot{V}O_2$ (7 fish), cardiac output (10 fish), haemodynamic parameters, and blood gas levels (18 fish) were measured on the 1979 trip, and effects of temperatures on blood gases (4 fish) and blood P_{50} (4 fish) were measured on the 1980 trip.

Catheters were implanted by removing a small skin flap over the subcutaneous artery and vein just caudal to the pectoral fin. The catheters were passed cephalad, as far as possible, via cutdowns in both the subcutaneous artery and vein. The venous catheter tip was located at the conjecture of the sinus venous and the atrium. The arterial catheter was advanced to the proximal portion of the dorsal aorta (Fig. 1) near the efferent branchial artery. This catheter was used to measure dorsal aortic blood pressure with a Statham P23DB transducer, remove samples for arterial blood gas determinations, inject tracer-labelled microspheres, and withdraw arterial blood samples for determination of cardiac output by dye dilution. The venous catheter was used to obtain samples for blood gas analysis and the injection of dye for cardiac output determination.

Blood pressure measurements were also made in the ventricle and bulbus arteriosus percutaneously with a 19 gauge needle connected to a Statham P23DB transducer. Heart rates were determined from phasic blood pressure measurements in the ventricle, dorsal aorta, and bulbus arteriosus for periods of up to 2 h after instrumentation. A measure of myocardial contractile function, dP/dt (mm Hg/s) of the heart was measured from the slope of the ventricular pressure traces at paper speeds of 100 mm/s.

Cardiac output measurements

Cardiac output measurements were made with an electromagnetic flowmeter (Biotronix, Model 610) in six fish, by dye dilution in four albacore, and with both methods simultaneously in one fish. Dye dilution was used to measure cardiac output in four fish where organ blood flow was determined. The flow transducers were placed around the ventral aorta which was dissected free just anterior to the bulbus arteriosus. In order to avoid occlusion of the coronary artery, which runs along the ventral aorta, the flow transducer (usually 4 mm internal diameter) was fitted around the vessel with the open key slot over the coronary artery. The dye dilution technique was similar to that used by Murdaugh et al. (1965).

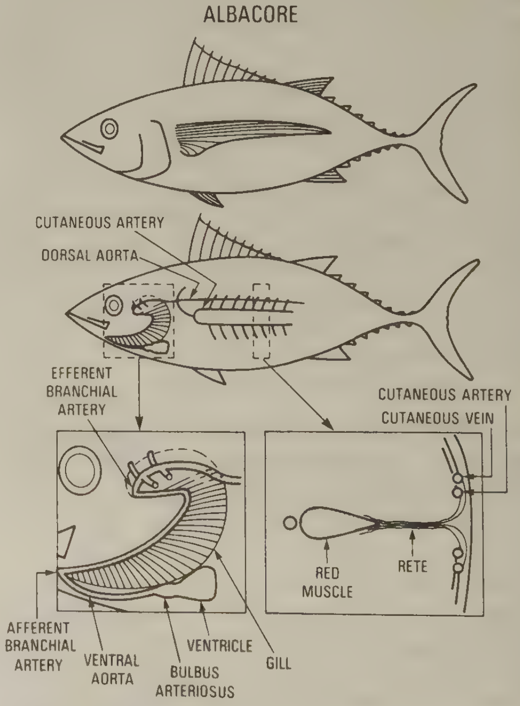

Fig. 1. Relative positions of the cutaneous arteries, veins, retia, heart, dorsal aortic and gills in *Thunnus alalunga*. The *left insert* shows the position of the efferent branchial artery where the tip of the arterial catheter would be positioned. The *right insert* shows the relative position of the red muscle, rete and cutaneous arteries and veins

The dye was injected into the subcutaneous vein and blood was withdrawn from the dorsal aorta. The electromagnetic flow meter technique in fish has been previously described by Johansen (1962).

Organ blood flow measurements

Organ blood flows were determined using tracer-labelled microspheres (^{141}Ce) injected into the dorsal aorta in four albacore showing spontaneous tail movement. Microspheres (15 ± 1 μm in diameter, New England Nuclear, Boston, Mass, USA) were suspended in 10% dextran with a small amount of Tween-80 detergent (0.05%) added to reduce clumping. The accuracy of blood flow measurements determined by microspheres is dependent on having a minimum of several hundred spheres per sample (Heymann et al. 1977). Neumann et al. (1983) found that fish white-muscle is sparsely perfused. We thus injected 2×10^6 microspheres into each albacore to be sure that white-muscle flow estimations could be made.

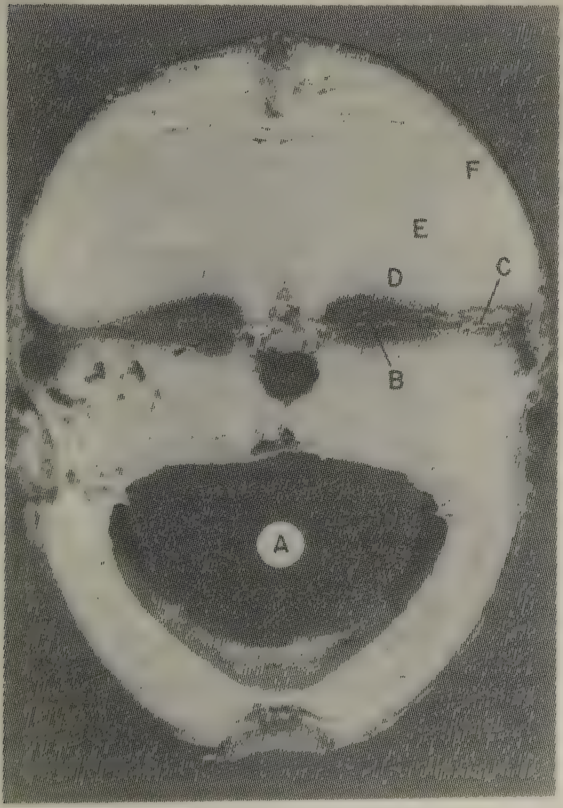

Fig. 2. Relative positions of white- and red-muscle from the midsection of the albacore tuna. *A* body cavity; *B* red-muscle; *C* rete; *D* inner white-muscle; *E* middle white-muscle; *F* outer white-muscle. *D*, *E* and *F* indicate sites of white-muscle sampling for blood flow measurements

The cardiac output and organ blood flow studies were carried out between 30 min and 1 h after the initial instrumentation. At the end of the experiments, the fish were sacrificed and tissue samples of about 20 g were taken from each organ. These were blotted and weighed, minced, immersed in formalin, and allowed to dry for several days. The pieces were then packed into counting tubes and assayed in a Packard Autogamma Spectrometer (5912A) by standard techniques (Heymann et al. 1977). Blood flow was determined to the red- and white-muscle in samples collected from the side of the fish contralateral to catheter placement. White-muscle samples were taken from the cephalic and caudal sections of the fish and each sample was divided into outer, middle and inner sections (Fig. 2). Red-muscle samples were then taken from the cephalic and caudal areas about the midline of the fish. The entire gill structure was also measured for radioactivity to determine if microspheres had lodged in this tissue. To ensure equal distribution of microspheres to organs of the viscera, the dorsal aortic catheter was inserted as far toward the head as possible (see Fig. 1). At the end of each experiment the position of this catheter was verified. The external diameter of the catheter was 1.0 mm while the internal diameter of the dorsal aorta at this site was about 2.0 mm. Thus sufficient blood flow for normal distribution was available.

The total activity of the microsphere suspension injected into each fish was calculated and regional blood flow was determined as follows:

Tissue flow = (Q × tissue cpm)/(injected cpm) where Q = cardiac output (ml/min), tissue cpm = counts per min in tissue samples, and injected cpm = counts per min of the injected microsphere suspension. Blood flow, expressed as ml/min/g, was computed by dividing tissue flow by the weight of each sample.

Temperature measurements

Needle thermistors were inserted into or near the centres of the red- and white-muscle mass of six fish within 5 min of capture. Temperatures were measured with a Yellow Springs Instrument (YSI), No. 513, thermistor probe and read on a YSI Model 41 Tele Thermometer.

Blood gas measurements were made in 18 fish, 7 of which were also used in $\dot{V}O_2$ studies. The effect of temperature on blood gases was determined by using two gas analysers set at the upper and lower temperature extremes experienced by albacore blood. One instrument (Instrumentation Laboratories, Model 213) was maintained at 22° C (ambient water temperature), while a second (Radiometer Model BMS-3) was set at 32° C, the highest red-muscle temperature likely to be encountered. Blood gas results, used in the $\dot{V}O_2$ calculations, were taken from one machine set at 25° C.

$\dot{V}O_2$ was calculated from the product of cardiac output and arterial-venous O_2 content difference. O_2 contents were calculated as the sum of dissolved plus haemoglobin-bound oxygen. The dissolved O_2 was calculated assuming a blood temperature of 25° C, and a plasma solubility given by the following relationship:
Solubility = 0.00595−0.0001266*T +
0.0000013*T2
where T is the temperature in ° C.

The haemoglobin-bound component was calculated using a standard relationship between tension and partial pressure (Kelman 1966), and using a measured haemoglobin P_{50}. Haemoglobin concentration was measured using the cyanomethaemoglobin technique. To avoid inaccuracies due to interference from erythrocyte nuclei, samples were centrifuged prior to measuring optical absorbance at 540 mn. Haemoglobin P_{50} was measured using a modification of the technique described by Neville (1974). Briefly, 0.1 ml of fresh blood was suspended in 1.6 ml of a yeast-buffer-glucose solution (tris-[hydroxymethyl] aminomethane buffer, 310 m0sm, pH 7.5) and measured by tonometer to a PO_2 of 300–400 Torr. This mixture was injected into a heated cuvette which included a Clark microelectrode fitted with a 0.8 mil polyethylene membrane to improve the response at low levels of PO_2. The mixture was warmed and the fall in PO_2 with time was recorded. The pH of the reacting suspension was measured anaerobically with a glass pH electrode (Radiometer). The P_{50} of the red cells was calculated from the rate of fall in PO_2 with time, and corrected to a pH of 7.4 using a blood gas slide rule (Severinghaus 1966).

Measured and calculated values for all parameters are presented as mean ± standard error of the mean. The student *t*-test was used to determine significance of the mean values between two groups. Differences were considered significant at $P < 0.05$.

Results

Heart rate

Heart rates, calculated from blood pressure measurements, were relatively stable over the 90 min periods of experimentation for each fish (Table 1), but varied considerably among the fishes, (69–150 beats/min). In five albacore a marked drop in heart rate, from 107±3 beats/min to 13±2 beats/min, was noted within 2 min of hypoxia (cessation of ventilation).

Table 1. Heart rate and blood pressure in *Thunnus alalunga*

HR		Ventricular (S/D) (mm Hg)		Bulbus (S/D) (mm Hg)		Dorsal aortic (S/D) (mm Hg)	
Time (min)							
30′	90′	30′	90′	30′	90′	30′	90′
135	133	100/7	55/6	98/75	55/40	78/72	40/38
136	142	112/5	89/4	110/93	75/60	89/85	60/58
76	73	90/8	60/4	90/65	60/36	71/68	45/42
69	73	107/3	105/8	105/80	100/80	96/90	76/72
150	130	90/2	73/5	88/70	70/50	–	–
133	136	100/6	88/5	98/75	–	–	–
120	120	–	89/7	–	–	–	–
136	130	120/10	–	–	–	112/108	70/67
125	95	–	–	–	–	90/84	85/82
136	–	–	–	–	–	68/60	–
120	–	–	–	–	–	–	62/53
142	–	–	–	–	–	77/72	–
$\bar{x}$ 115	115	103/6	79*/6	98/78	72*/53*	84/78	57*/59*
± 5	5	3/1	7/0.05	3/4	8/8	5/5	10/6

S/D Systolic/Diastolic; ± ±SEM (standard error of mean); * Significant $P < 0.05$ compared to 30′; Pressures are given as mm Hg

Table 2. Cardiac output and stroke volume in *Thunnus alalunga*

Fish	Mass (kg)	CO (ml/min)	CO^{1} (ml/min/kg)	HR (beats/min)	SV (ml)	Method
1	11.2	320	28.6	99	3.2	DD
2	9.8	340	34.7	120	2.8	DD
3	10.1	362	35.8	142	2.5	DD
4	9.9	280	28.3	79	3.5	DD
4	9.9	273	27.5	82	3.3	EM
5	7.8	374	47.9	104	3.6	EM
6	8.1	194	24.0	89	2.2	EM
7	7.4	458	61.9	77	5.9	EM
$\bar{x}$	9.3	325	36.1	99	3.4	
±SEM	0.5	30	5	8	0.4	
(Standard error of mean)						

CO Cardiac output; *HR* heart rate at the time of cardiac output measurement; *SV* stroke volume, calculated as $\frac{CO}{HR}$;

DD dye dilution; *EM* electromagnetic flow transducer; *CO*^{1} normalized cardiac output $\frac{\text{CO (ml/min)}}{\text{Mass (kg)}}$

Blood pressures

Systolic and diastolic blood pressures measured in the ventricle, bulbus arteriosus, and dorsal aorta at 30 min and 90 min after the fish were prepared for experimentation, are presented in Table 1. Highest blood pressures were measured in the ventricle during systole, mean 103±3 mm Hg ($n=7$). During diastole there was a marked drop in pressure in the ventricle, mean 6±0.05 mm Hg ($n=7$). Systolic pressures in the bulbus arteriosus, mean 98±3 mm Hg ($n=6$), were almost identical to those in the ventricle, suggesting little pressure drop across the valve. However, bulbus diastolic pressures, mean 78±4 mm Hg ($n=6$), were higher than in the ventricle as would be expected: the former is the true diastolic pressure in the arterial system while the latter is a measure of preload in the ventricle. The mean systolic pressure in the dorsal aorta was 84±5 mm Hg ($n = 8$), which represents an approximate 14% drop in pressure across the gills. During diastole only slight decreases in pressures were recorded in the dorsal aorta, mean 78±5 mm Hg ($n=8$), which is identical to the mean diastolic pressure measured in the bulbus arteriosus.

There was a gradual, but marked decrease in systolic pressures during the experimental period. At 90 min the mean systolic pressures in the ventricle ($n=7$), bulbus arteriosus ($n=5$) and dorsal aorta ($n=7$) were 79±7, 72±8 and 57±10 mm Hg, respectively. These values are significantly lower ($P<0.05$) than those recorded at 30 min. Diastolic pressures in the bulbus arteriosus and dorsal aorta decreased to 53±8 and 59±6 mm Hg, respectively, at 90 min, which are significantly lower ($P<0.05$) than at 30 min. The contractile force of the heart, dP/dt (mm Hg/s), was measured in four albacore at 6342±822 mm Hg/sec.

Cardiac output

Cardiac output data from seven fish are given in Table 2. Fishes 1–4 had cardiac output determined by dye dilution. Electromagnetic flow-transduced cardiac output measurements were made in fish 4–7. Both measurements were made in fish 4 and are in good agreement. Stroke volume showed some variation among fish which could not be accounted for by differences in body mass or heart rate, although there was generally an inverse relationship between heart rate and stroke volume. Cardiac output varied greatly between fish of nearly equal mass, due to differences in heart rate and stroke volume. The mean cardiac output was 36.1±5 (ml/min/kg).

Organ blood flow

Microsphere measurements showed considerable differences in blood flow rates (ml/min/g) to different organs of the body (Table 3). The highest flow was to the kidneys, 0.42±0.07 ml/min/g, and the smallest was to the white-muscle, 0.01±0.005 ml/min/g and to the skin, 0.01±0.005 ml/min/g. Blood flow to white-muscle ranged from 0.029±0.04 ml/min/g (in the inner portion of the fish) to 0.006 ml/min/g (in the midregion of the tail) (Table 4 and Fig. 2). Blood flow measurements as low as 0.003 ml/min/g represent negligible flow and are within the permitted error of the method. Blood flow to red-muscle

Table 3. Organ blood flow in *Thunnus alalunga*

Tissue	Organ Mass (g)	% CO	Flow (ml/min/g)
Red-muscle	452 ± 30	36.2	0.22 ±0.04
White-muscle	5950 ±290	27.5	0.013±0.005
Stomach	136 ± 8	2.8	0.057±0.007
Intestine	28.7± 2	1.8	0.17 ±0.06
Spleen	17.5± 0.5	1.4	0.22 ±0.06
Kidney	45 ± 5	6.7	0.42 ±0.07
Liver	243 ± 16	13.0	0.15 ±0.02
Skin	65 ± 2.1	0.2	0.01 ±0.005

Mean ± SEM (standard error of mean); *N* = 4; Mean body mass = 9.8 ± 0.34 kg; *CO*, cardiac output

Table 4. Regional flow in the white-muscle of *Thunnus alalunga*

	Cephalic	Caudal
Inner	0.029 ±0.04	0.004** ±0.0003
Mid	0.009* ±0.003	0.0006** ±0.0002
Outer	0.004* ±0.006	0.003** ±0.0005

Mean ± SEM (standard error of mean); Flow in ml/min/g; * Significant *P* <0.05 compared to inner; ** Significant *P* <0.05 compared to cephalic

and spleen were relatively high and identical 0.22±0.04 ml/min/g. Lesser flow rates were recorded to the intestine, 0.17±0.06 ml/min/g, and liver, 0.15±0.02 ml/min/g. A relatively low rate of flow was measured in the stomach, 0.06±0.007 ml/min/g.

Table 6. Oxygen consumption of *Thunnus alalunga*

Fish	Arterial-venous difference (ml O_2/dl)	$\dot{V}O_2$ (ml O_2/min/kg)
1	9.4	2.7
2	12.0	4.2
3	5.6	2.0
4	6.6	1.9
5	9.8	4.7
6	8.4	2.0
7	10.8	6.7
x̄	8.9	3.4
±SEM (Standard error of mean)	0.9	0.7

Same fish as Table 2; $\dot{V}O_2$ calculated as: (cardiac output x arterial-venous difference); $\dot{V}O_2$ = oxygen consumption

Blood gases, oxygen consumption, and body temperature

Blood gas data are contained in Table 5. Arterial PO_2 was 62.0±2.9 Torr and decreased to 14.3±1.2 in venous blood. The arterial blood was significantly more alkaline than the venous blood. Haemoglobin volumes were 15.8±0.1 which is equivalent to a haematocrit of 47.5. Arterial-venous oxygen content difference and oxygen consumptions are given in Table 6. The mean oxygen consumption was 3.4±7 (ml 0_2/min/kg). The effects of temperature on blood gases are given in Table 7. Arterial and venous blood samples from each fish were run at different temperatures in separate blood gas machines. Both arterial and venous blood, had PO_2's which were higher in cooler blood. There was no temperature effect on CO_2 tension but the blood was more alkaline at lower temperatures in both arterial and venous blood. The average P_{50} was 15.9 Torr at a temperature of 37° C and pH of 7.4.

Temperature measurements in red-muscles were made at three time periods: 10–15 min after landing, 30 min, and 90 min. The initial red-mus-

Table 5. Blood gases and O_2 content in *Thunnus alalunga*

Fish	Arterial						Venous				
	PO_2 (Torr)	PCO_2 (Torr)	pH	O_2 Cont (ml O_2/dl)	SAT (%)	Hb (g/dl)	PO_2 (Torr)	PCO_2 (Torr)	pH	O_2 Cont (ml O_2/dl)	SAT (%)
1	68.1	5.6	7.846	21.9	99.4	16.0	14.5	10.5	7.479	12.5	56.9
2	57.5	4.9	7.533	21.7	98.6	15.5	12.1	10.0	7.444	9.7	44.4
3	56.2	3.5	8.038	21.9	99.4	15.4	18.2	6.5	7.522	16.3	74.5
4	70.0	3.8	7.850	22.0	99.5	16.1	17.9	11.9	7.498	15.4	70.4
5	50.5	3.2	7.944	21.4	99.2	15.4	11.3	7.6	7.690	11.6	54.4
6	70.6	3.0	7.807	21.5	99.5	15.7	16.0	10.0	7.440	13.1	60.7
7	61.4	5.0	7.964	21.5	99.4	16.2	9.8	6.6	7.748	10.7	49.9
x̄	62.0	4.1	7.855	21.7	99.3	15.8	14.3	9.0	7.546	12.8	58.7
±SEM (standard error of mean)	2.9	0.4	0.62	0.1	0.1	0.1	1.2*	0.8*	0.046*	0.9*	4.1*

Temperature 25° C; O_2 Content in ml O_2 per deciliter of blood; *SAT* saturation in %; *Hb* haemoglobin in grams per deciliter; Gas tension in Torr; * Significant *P* <0.05 venous compared to arterial values

Table 7. Effects of temperature °C on blood gases of *Thunnus alalunga*

Fish	PO_2 (Torr)				PCO_2 (Torr)				pH			
	A		V		A		V		A		V	
	32°	22°	32°	22°	32°	22°	32°	22°	32°	22°	32°	22°
1	39.5	52.6	17.2	18.7	3.0	3.0	5.6	5.6	7.73	8.03	7.55	7.84
2	60.0	67.6	12.2	13.2	2.6	2.6	4.5	8.8	7.55	7.86	7.29	7.49
3	40.0	58.7	6.0	8.1	4.4	4.4	3.2	5.0	7.65	8.02	7.76	7.96
4	26.0	30.1	7.3	7.6	3.3	3.3	10.0	5.8	7.57	7.85	7.57	7.85
$\bar{x}$	41.4	52.3	10.7	11.9	3.3	3.3	5.8	6.3	7.63	7.94	7.54	7.79
±SEM (standard error of mean)	7.0	8.0*	2.6	2.6*	0.4	0.4	1.4	0.9	0.04	0.05*	0.10	0.10*

* Significant $P < 0.05$ 22°C vs. 32°C paired *t*-test; *A* arterial; *V* venous; the temperature (°C) of blood gas machine 1 was 22°C and bloodgas machine 2 was 32°C

cle temperature was 28.9° ±0.8° C, at 30 min, 26.9° ±0.7° C and at 90 min, 24.7° ±0.9° C. The water temperature of the holding tank was 21.9° ±0.1° C and the surface sea water temperature was 21.3° ±0.1° C.

Discussion

Heart rate and blood pressure

Reported heart rates in fishes usually range from 25–70 beats/min (Randall 1970). The heart rate of swimming salmon has been measured as high as 100 beats/min (Smith et al. 1967). Heart rates in our study had a very wide range (69–150 beats/min), but the albacore, in which only heart rates and blood pressures were measured (Table 1), had mean heart rates of 115±9 beats/min. These heart rates remained relatively constant over several hours despite decreasing red-muscle temperatures and decreasing blood pressures. Temperature, vagal tone and hypoxia all may have a marked influence on the heart rate of fishes (Randall 1970; Stevens 1972). Hypoxia was probably not a major factor in heart rate measurements in most of the albacore because arterial PO_2 was maintained higher than 60 Torr. As in other species, induced acute hypoxia caused bradycardia in five albacore. The heart rates seen in this study are higher than those reported by Stevens (1972) of 70 beats/min in the restrained skipjack tuna. But Stevens also reported a large variation in heart rate during the experiments (46–142 beats/min) which he attributed to differences in vagal tone. Brill (1987) reported heart rates in skipjack and kawakawa of over 200 beats/min under experimental conditions similar to this study.

Our recordings of ventricular pressures of 98±3 mm Hg are higher than that reported in other teleosts (Randall 1970). Randall et al. (1965) reported ventricular pressures in freshwater fish of approximately 40–45 mm Hg, and in the Pacific salmon Robertson et al. (1966) reported ventral aortic pressures of approximately 80 mm Hg. We observed a systolic pressure drop (20 mm Hg) across the gill which is similar to that reported by other investigators (Hanson 1967; Holeton and Randall 1967; Lai et al. 1987). The high heart rates and blood pressures are physiologic evidence of high cardiac performance. The data from this study showed a relatively high contractile force in the heart (over 6000 mm Hg/s). This high contractile force combined with the filling pressure of 6 mm Hg, can take advantage of the Starling effect which would dictate a relatively high stroke volume. It has been shown that increased filling pressure combined with the increased contractile force of the heart contributes to higher stroke volume (White et al. 1987). Normal mammalian measurements of dP/dt in pigs (White et al. 1987) are 2000 mm Hg/s, which increase to about 8000 mm Hg/s during intense exercise. It appears that the albacore ventricular contractile force is equivalent to that of mammals. Breisch et al. (1983) showed that the albacore myocardium is composed of 82% spongy mass and 18% compact myocardium. It is unlikely that only 18% of the myocardium is responsible for the relatively high amount of cardiac work seen in this fish. Therefore, it is probable that the spongy myocardium provides a considerable force for the ejection of blood and the generation of high ventricular pressures. Further investigations of the force generated by the spongy myocardium are needed to understand fish ventricular mechanics.

Cardiac output and oxygen consumption

Both methods of measurement used in this study, dye dilution and the electromagnetic flow transducer, have been used in fish previously. In our experiments, both methods seem comparable: however the dye technique was simpler to use, and the effects of opening the pericardium in order to implant the electromagnetic flow probe around the ventral aorta, could have a deleterious effect on cardiac function (Lai et al. 1987). Resting cardiac outputs have been measured in a number of fish species. Values in the trout range from 18 ml/min/kg (Kiceniuk and Jones 1977) to 45 ml/min/kg (Neumann et al. 1983). Using the electromagnetic flow probe, Johansen (1962) measured a cardiac output of 9.3 ml/min/kg in the cod. Murdaugh et al. (1965), using dye techniques, measured a cardiac output of 26.7 ml/min/kg in *Squalus acanthias.* Our measurements of about 34 ml/min/kg appear to be not unusual for a teleost and are very similar to that reported in the albacore by Lai et al. (1987). But we must be cautious on any interpretation of the cardiac output in a partially anaesthesized and traumatized fish compared to one that is free swimming. $\dot{V}O_2$ data given in this paper are similar to that given by Graham and Laurs (1982) for albacore swimming in a respirometer.

Organ blood flow

The microsphere method allowed several observations to be made about organ blood flow in the albacore. However, this method was limited because of the unavailability of a suitable catheter location to distribute microspheres to the heart and brain. Since both the heart and brain are perfused by arteries coming from the efferent branchial arteries, no microspheres reached these organs. The relative and absolute blood flows to various organs are similar to those reported in the Arctic grayling (Cameron 1975), although the kidney and the spleen flows are somewhat lower and higher respectively. White-muscle blood is sparse but there is a heterogenous flow of blood to this organ. We found that white-muscle blood flow was highest nearest the red-muscle and decreased to near zero in the caudal direction. This is in agreement with the finding of Cameron (1975) that the highest white-muscle flows were in the cephalic direction. These data may support the concept that tuna white-muscle possesses a greater potential for aerobic metabolism, particularly in the region where temperatures are elevated. Graham et al. (1983) suggested that white-muscle activity partiall assumes red-muscle function where the temperatures are elevated. Our finding that the inner white-muscle has increased blood flow further supports the concept of a mixed function and morphology for albacore white-muscle.

Red-muscle received the highest percentage of the total cardiac output, approximately 36%, although this organ represents less than 5% of the fish mass. The rate of blood flow to the white-muscle was quite low, but due to its large mass, occupying more than 60% of the total mass of the fish, the white-muscle received almost 28% of the cardiac output. The liver, which accounts for 2.5% of the total body weight, received 13% of the cardiac output. The kidney, while comprising only 0.5% of the total body weight, received 6.7% of the cardiac output. The stomach received less than 3% of the cardiac output, the intestine and spleen each received less than 2% and the skin less than 0.2%. Our measurements account for 89.6% of the cardiac output. Microspheres in the gills account for another 5% of the total injected. We asume that the remainder, approximately 4.5%, found its way to tissues that were not assayed (bone, heart, brain, and other organs). These tissue blood flows are similar to those found in mammals.

Blood gas measurements

The blood gas measurements presented here are markedly similar to those of Jones et al. (1986) in the free swimming tuna, *Euthynnus affinis* (kawakawa). Cech et al. (1984) clearly showed a reverse temperature effect of lowering arterial PO_2 with warming in the albacore, while Jones et al. (1986) showed a positive temperature effect in the kawakawa. Our data confirm the reverse temperature effect on PO_2 in albacore and show a decrease in pH with increasing temperature. However, we could not see marked temperature effects on CO_2, perhaps because of the narrow range of CO_2 values in the blood. Our P_{50} value of 15.9 Torr is lower than that reported by either Cech et al. (1984) or Jones et al. (1986). However, this value is not unreasonable given that the average venous PO_2 we observed (Table 5) was 14.3 Torr at 25° C

In conclusion these data show that the albacore tuna is capable of relatively high cardiovascular performances and blood flows which are similar to those in mammals.

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Appendix 3

BOWHEAD POPULATION ESTIMATE AND VARIANCE

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As indicated in SC/39/PS7, likely upward bias in the 1986 population size estimates in Table 7 of that paper preclude their use in assessing the size of the stock. Sub-committee discussions have pointed to the estimates 8,778 and 5,641 as the most acceptable estimates among those presented for 1985. Clear sources of bias (for example, the failure to account for unmonitored hours) suggest that the other 1985 estimates in Table 7 should be eliminated.

It would be desirable to have independent evidence that the tracking parameters used produce unbiased counts of whales. Separate studies of bowhead migration behaviour indicate a reasonable range of speed and direction parameters but provide only limited help in setting these parameters for a particular part of a particular season.

We therefore depend on the visual census to guide our choices. The tracking parameters which result in the estimate 8,778 also produce counts of visual tracks which match the observers' counts of new whales plus half the conditional whales. The tracking parameters which produce the estimate of 5,641 result in a somewhat better match between speed and direction distributions computed from tracks and from duplicate sightings made by the visual census.

Thus we cannot be sure which of these estimates is most unbiased. We therefore propose their average (7,200) as our current best estimate of the size of this stock. A jack-knife variance estimate was suggested by Chapman. Such an estimate, conditioned on the assumption that the tracking algorithm counts duplicates correctly, was computed from the data which produced the estimate 5,641. We were not able to compute a variance for the larger estimate because we did not have all the necessary data at this meeting.

The jack-knife variance estimate we use is given by (18) and (19) of Zeh *et al.* (1986, *Rep. int. Whal. Commn* 36: 317–23). We have 35 time periods of varying length with acoustic and/or visual watch in the 1985 season*. We can therefore obtain 35 different population estimates by omitting each period in turn from our calculations. The appropriate average of these provides a variance estimate which reflects the effect of omission of each period on the mark-recapture estimates of whale numbers and detection probabilities, the estimates P_3, and interpolation for unmonitored hours. The estimated standard error obtained by this method is 1,900. We believe this provides a reasonable measure of the variability of the estimate 5,641.

The standard error reported above indicates a coefficient of variation of 34% which we assume is applicable to the mean estimate of 7,200. We therefore propose 7,200 ± 2,400 (where 2,400 is 1SE) as the current best population size estimate.

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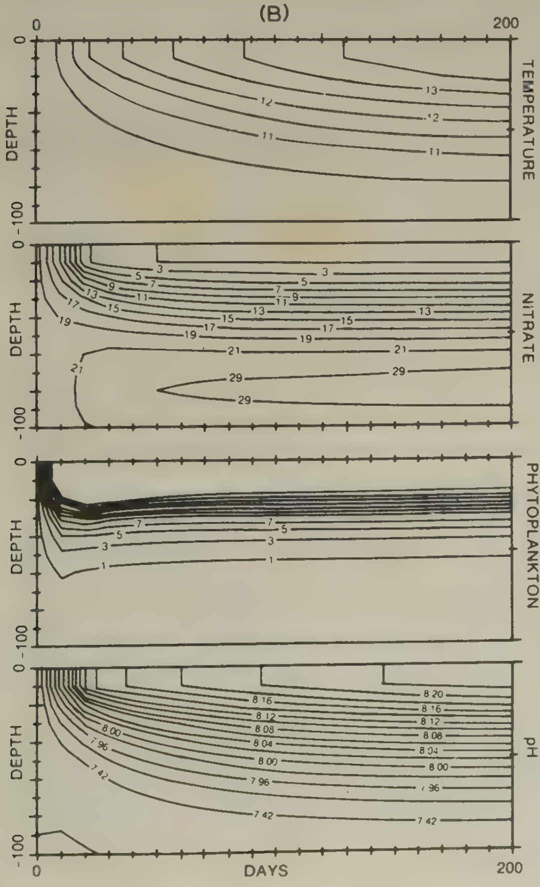
* Our 35 time periods take the role of the watched days in equations (18) and (19).

for 200 days: *low mixing*, with no upwelling and 2 m s^{-1} surface winds (Fig. 7A), and *high mixing*, 0.5 m day^{-1} upwelling and 5 m s^{-1} surface winds (Fig. 7B). Initial conditions are uniform profiles representing cold, deep water with low phytoplankton, low pH and high nitrate concentration. Low mixing, after 10 days, produces a mixed layer above a strong thermocline that continually deepens. A surface phytoplankton bloom peaks between 20 and 30 days and then declines, leaving a subsurface phytoplankton maximum, when nitrate is depleted in the mixed layer. High mixing produces a weaker thermocline which, because of upwelling, is more shallow than the first case. The surface phytoplankton bloom reaches a higher peak that declines more slowly. The vertical maximum phytoplankton biomass remains at the surface.

Figure 8(A, B) shows phytoplankton–temperature and pH–temperature plots from the two model runs. Since the model run was arbitrarily set to start at 10°C, differences in absolute temperature between the model run and the waters of the Gulf are not important. Although the two plots represent covariability in time, the same relationships will be observed in the spatial domain



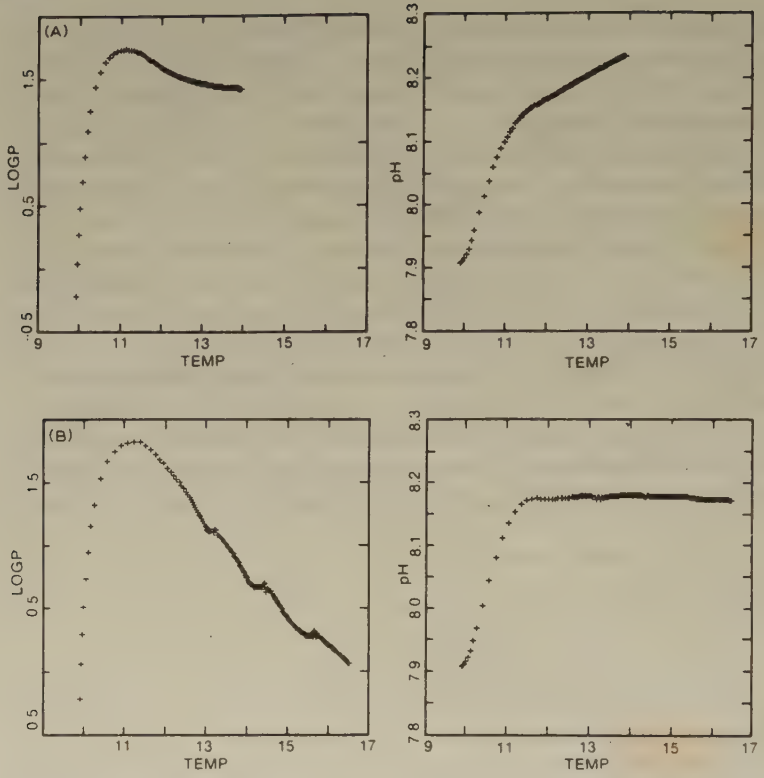


Fig. 8. Results of model simulation for surface waters. (A) Plots of log pigment and pH vs. surface temperature for high mixing condition. (B) Plots of log pigment and pH vs. surface temperature for low mixing condition.

if spatial variability is caused by asynchronous temporal cycling. Such asynchrony might be caused by upwelling at capes and banks or by local mixing events such as storms or breaking internal waves.

The most obvious feature of both plots for both runs is the break at 11–11.5°C. In this temperature range, nitrate drops to levels that significantly limit phytoplankton growth. Phytoplankton increases up to this temperature and then decreases above it. The negative slope of the phytoplankton–temperature plot above 11.5°C is much steeper in the low mixing run because mixed layer nitrate is lower and phytoplankton growth does not compensate for grazing and diffusion losses.

Initial pH in these runs corresponds to oversaturation of CO_2. Atmospheric equilibrium is not attained in either run. Phytoplankton growth accelerates the approach to equilibrium as the surface water warms. Thus, the different slopes of the pH–temperature plots above 11.5°C represent the different growth rates maintained after the initial surface bloom. In the high mixing run (Fig.

8A), pH continues to increase because nutrient input by upwelling and diffusion across the thermocline are sufficient to support continued net carbon fixation by photosynthesis. If the lapsed warming time of the water is substituted for the water temperature in Fig. 8, then the slope of the pH–time plot represents the net CO_2 fixed over the 200 days (minus the CO_2 lost by evasion). Of the two cases illustrated, the results produced by the low mixing case (Fig. 8B) more clearly resemble the plots obtained from the satellite imagery and underway data. The steep decrease in phytoplankton and leveling off of pH at higher temperatures suggest that stratification in the southern Gulf is instrumental in controlling production.

The satellite observation did not show the cold temperature (left) portion of the log pigment–temperature plot predicted by the model. This was as expected, since deep water, devoid of phytoplankton, does not instantaneously surface, as in the model. However, the imagery shows essentially constant phytoplankton over 4° of warming ($\sim$40–60 days). This suggests that the model does not fully simulate the observed conditions. Be that as it may, it is not our intention to model the Gulf of California accurately (a much more complete set of experimental data would be needed), but to point out that a comprehensive approach may serve to explore relationships among temperature, pH and chlorophyll on large spatial scales, with the ultimate purpose of assessing oceanic primary production remotely.

Finally, the examples presented here qualitatively illustrate how productivity rates, relative to the rate of heating of the surface water, are represented by the slopes of the phytoplankton–temperature and pH–temperature curves. To the extent that these surface variables change through biological responses to physical mixing, they can yield information about vertical movements within the near-surface water column. Thus satellite measurements of surface temperature and chlorophyll may also yield information about near-surface vertical structure.

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